THE QUARTERLY REVIEW *of* BIOLOGY

VOLUME III
1928

Published by
THE WILLIAMS & WILKINS COMPANY
BALTIMORE
U. S. A.

THE QUARTERLY REVIEW OF BIOLOGY

RAYMOND PEARL, *Editor*
The Johns Hopkins University

ASSISTED BY

R. W. HEGNER, *Contributing Editor*
BLANCHE F. POOLER, *Assistant Editor*
JOHN RICE MINER, *Assistant Editor*
The Johns Hopkins University

ADVISORY BOARD

CONTENTS

No. 1, March, 1928

No. 2, June, 1928

No. 3, September, 1928

No. 4, December, 1928

Photo by Spencer and Wyckoff

"FELLOW"

Vol. III, No. 1 March, 1928

THE QUARTERLY REVIEW of BIOLOGY

THE SENSORY CAPACITIES AND INTELLIGENCE OF DOGS, WITH A REPORT ON THE ABILITY OF THE NOTED DOG "FELLOW" TO RESPOND TO VERBAL STIMULI

By C. J. WARDEN and L. H. WARNER
Animal Laboratory, Department of Psychology, Columbia University

THE material selected for discussion in this paper naturally falls into two major divisions as indicated in the title. The attempt is made in the first general section to present, very briefly indeed, a fairly systematic account of the more important aspects of the capacities and behavior of the dog, insofar as these have been revealed by careful observation and experimental analysis. Vastly more information is at hand on the sensory capacities of the dog than on what we usually think of as general intelligence. The sections covering such capacities, especially visual, olfactory and auditory, are accordingly large while that on intelligence is correspondingly small. The distinction here made is, of course, one of convenience only, inasmuch as general intelligence must be, in the very nature of the case, a function of sensory and other capacities. A short section treating of the special fitness of the dog to serve as a subject for extensive and intensive behavior studies in the modern animal laboratory will follow that on intelligence. The second major division of the paper will consist of a fairly detailed account of certain tests, recently conducted by the writers, on the German Shepherd Dog "Fellow"—widely known on stage and screen—to determine to what extent, if any, his reputed ability to understand human language is justly warranted.

Before entering upon the main discussion it may be not entirely out of place to remind you that the attitude of the modern comparative psychologist is one of healthy skepticism toward supposed cases of animal genius and human-like levels of animal intelligence. It is not that the student of animal behavior has a grudge against the infra-human kind, or any scientific or philosophical objection to a high evaluation of their abilities. For, in point of fact, no one more than the comparative psychologist welcomes evidence tending to confirm his belief in the essential continuity of all living forms on the

mental, as well as the physical side. He merely insists more emphatically than formerly that evidences of this character must run the usual gauntlet of scientific criticism; that claims of this sort must first be established by the most painstaking and defensible scientific methodology.

Much of what the average man "knows" about his own dog, and about dogs in general is, of course, quite unknown to the animal psychologist. For no animal has a richer heritage of lore, sentimental and lofty, representing an accumulation of the long ages since primitive man first made the dog his hunting companion and his domestic ally. It is difficult for any of us to escape entirely this traditional influence; most difficult indeed to observe with clarity of purpose and uncompromising logic the behavior of a dog, or other pet, to which we have formed an attachment. Only a few decades ago, and even in certain circles now, the method of anecdote with its unfailing tendency toward anthropomorphic interpretation stood in high favor, and passed itself off under the guise of science. Selecting cases to bolster up a theory may be an interesting diversion but it is hardly worthy of the trained mind in any field. We have deliberately eliminated from the following discussion all anecdote and have meant to include only such observational and experimental results as appeared to us to be worthy of the attention of the serious scientist.

I. SENSORY CAPACITIES AND INTELLIGENCE

Visual capacity

Consideration of the experimental literature on the visual capacity of dogs indicates that the average dog has far more faulty vision than most dog-lovers suppose. Behavior evidence for this conclusion is supported by anatomical study of the eye. Slonaker (43) reports that the dog possesses no fovea and that even the so-called "sensitive areas" are only vaguely defined. Numerous opaque nerve fibres are said to penetrate the retina, and these must be considered as blind spots. The pupillary opening is always relatively large and the pupillary response, while rather quick, is not strong. Johnson (22) and others have demonstrated convergence.

The method ordinarily used in testing the dog's eyesight has been called the discrimination method, and in most cases involves the use of the original "discrimination box" designed by Yerkes and Watson (58), or some modification of this. The dog being tested is faced with a choice of two alleyways, the one leading to a compartment in which he will find food, the other to a compartment where he is usually given a light electric shock. Whether or not the dog makes a fortunate choice he is faced with this situation again and again. Sometimes the reward is to the right and the punishment to the left, sometimes just the reverse. The only way the animal can be sure of making a correct choice is by attending to signals or cues (stimulus patches) which are presented at the entrance of the alleyways. In testing for brightness discrimination, for example, a very bright light may be placed always at the entrance of whichever alley in that trial leads to the food, a less bright light at the other alley entrance. Many precautions must be taken to insure the fact that there are no other stimuli than the signals being studied which might give the animal a clue as to which alley to enter. Use of his nose to detect the side of the box at which he will receive food will not help the dog for there is food in both compartments, though in the punishment compartment it is screened off so as to be inaccessible. The experimenter must be entirely eliminated

from the situation, for the dog, more perhaps than any other animal, is quick to take advantage of the to us almost imperceptible movements that the onlooker often and quite unwittingly makes in indication of the correct direction.

This method has been used in the study of brightness, size, and form discrimination in the dog but not, as yet, in the study of color discrimination. Under adequate experimental conditions positive results as obtained by this method may be accepted as final, but it is to be noted that negative results cannot be considered conclusive, since it is conceivable that an animal might be capable of somewhat more delicate discriminations in a less arbitrary or complex situation.

Szymanski (51) used this general method in studying brightness discrimination. His dogs were a cross between a Spitz and a fox terrier. His results were entirely negative for slight differences in brightness. Only when one alley was brightly lighted and the other entirely dark was he able to get a discrimination habit. Very similar results were obtained by Sutherland (46) using the same method. His dogs, mongrels, discriminated between a light and no light, but not between one light as opposed to two lights, or even as opposed to four lights. Form as well as brightness discrimination would have been involved in these cases of course, since the bulbs were actually in view. Stone (45), however, using a male and a female fox terrier found evidence for a much finer degree of brightness discrimination. Having built up a discrimination habit for two lights differing considerably in brightness he gradually reduced the intensity of the brighter until a point was reached where the habit broke down. He then increased the difference between the two lights until the habit was reestablished and again gradually approached the threshold value. Stone also tested three human subjects by the same method—except, of course, that these subjects indicated by word of mouth rather than by turning to the right or left which light was in their opinion the brighter. The men could, on the average, distinguish a light of 1 c.p. from 1.1 c.p. The male dog discriminated between a 1 c.p. and a 1.2 c.p. light, while the female dog did slightly better. The dogs were thus inferior to the men, but only slightly so.

All the work on form and size discrimination except that of the Russian school is in accord with the conclusion that the dog is very deficient in these respects. Johnson (23), using an English bull terrier, was unable to establish evidence for discrimination between vertical and horizontal lines, these lines, alternately black and white, being 3.9 mm. wide on a circular field 6 cm. in diameter. Skiascopic examination of the dog's eyes, both with and without mydriatic, seemed to indicate that objects at a distance of twenty feet or more, i.e., at a distance such that the light rays were approximately parallel, were focussed on the retina. Nothing is known of the ability of the dog to accommodate, and thus it might have been that failure to discriminate in Johnson's case resulted from inability to focus upon objects so close to the eyes as the signals were placed. Johnson considered overcoming this difficulty by equipping the dog with a pair of spectacles. Instead, however, he introduced a system of lenses before the signals in such a way as to throw the light reflected from them onto the dog's eyes in parallel rays. But even with all these advantages that science offered the dog did no better. It could not even distinguish between a plain field and one of black and white stripes, 3.9 mm. in width. Each of these stripes subtended a visual angle of 33′ 32″ or an

angle larger than that subtended by the sun's disc at the earth. Johnson states that this coarsely striped field is "closely comparable with that of a plank fence, the units of which are 6 inches wide and 6 inches apart, viewed at a distance of 50 feet." Most dog-lovers would refuse to believe that their pets were incapable of such a discrimination.

Data on form vision have been reported by Williams (56) and by Szymanski (51). In neither case were the experimental conditions so admirably controlled as in Johnson's study. Williams was unable to establish discrimination between a square and a circle of equal area, although he did find discrimination between a constant and an intermittent light, the latter flashing at 2 second intervals. Szymanski was unable to establish response to a white pyramid standing in bold relief against a black background.

Johnson alone of American workers has studied size discrimination (22). His dog apparently discriminated between a circle 6 cm. in diameter and circles with diameters of 1, 2, and 3 cm. respectively. The 4 and 5 cm. circles were not certainly discriminated from the 6 cm. circle. The intensity of the light transmitted through the pairs of circles used was always constant. Thus it was impossible to say whether the animal's success was due to size discrimination or to luminosity. To test this matter Johnson equated the 6 and the 3 cm. circles for luminosity by reducing the larger circle to 25 per cent of its original brightness. As a result the dog no longer discriminated, choosing now one and now the other circle. His discrimination had therefore been based on luminosity differences.

The students of Pavlov, working in Leningrad, have reported data bearing on the sensory capacities of dogs. Unfortunately we are at present largely dependent on secondary source material, and thus a critical evaluation of the Russian work cannot readily be made. The method employed is quite different from that used by these other investigators, and the work still awaits verification in other laboratories. It involves the establishment of a conditioned salivary response to a given stimulus, as for example a black patch, by presenting this stimulus and the unconditioned stimulus, food, simultaneously a large number of times. After this conditioning is firmly established a second stimulus to be discriminated from the conditioned stimulus (a white patch, for example) is presented. Food is never presented with the white patch, whereas the black patch is often reenforced by the simultaneous presentation of food. Such training finally results in a differential response to the white and to the black patch, each presented alone, the one causing secretion of saliva, the other inhibiting such secretion, provided, of course, the sensory capacity of the dog is such as to permit such discrimination. Not only the visual capacity of the dog, but its auditory, olfactory, thermal, tactual, and gustatory capacities have been studied to some extent by this method. In general it may be stated that where the results of the Russian workers and those of other investigators are not in agreement, the findings of the former group seem to indicate greater sensory capacity. There are at least two possible explanations for these discrepancies. The salivary response method may be a more delicate measure of discriminatory ability involving, as it does, a more simple learning problem. On the other hand it may very well be that, due to technical errors in the application of the method, the dogs studied by the Russian students were responding to secondary criteria. That the latter is true of much of the

earlier Russian work seems evident. H. M. Johnson has subjected such studies to rigorous criticism. Partly as a result of such criticism, no doubt, radical changes have more recently been made in the technique employed by Pavlov's students. Whether or not these sufficed to entirely eliminate secondary clues cannot be said with our present indirect knowledge of their procedure. They have, apparently, succeeded in eliminating the experimenter from the situation, but this has necessitated the introduction of complicated mechanical devices for the presentation of the stimuli, which in themselves may conceivably offer secondary cues. It seems necessary, then, for us to present their results, largely on the basis of their report in Pavlov's recent volume, *Conditioned Reflexes* (35), with the hope that it will not be long until their experiments are known to us in greater detail and furthermore, have been verified in other laboratories.

Concerning the discrimination by the dog of intensity and luminosity differences the Russian work supports the results of Stone (45) mentioned above, who found greater acuity in this respect than any other investigator excepting the Russians. Frolov (35) using the Zimmermann series of grey papers, ranging from white to black, found the dog studied to be slightly superior to human beings, whereas Stone, using a different breed of dog, found them only slightly inferior to man. With respect to the discrimination of form and size, Orbeli reports results conflicting radically with those of other workers, since they seem to indicate discrimination of a large letter T from such forms as a square, a circle and so on. The luminosity and size factors, however, were apparently uncontrolled. It seems that the work on size discrimination must be thrown out on the same grounds. Furthermore, Orbeli's work was done in 1907 before the improved technique was introduced (57) in Leningrad. The work of Shenger-Krestovnikova (35) reported in 1921 cannot be criticised on the grounds of failure to control luminosity, since this investigator used figures constant in area and intensity, differing only in form. The two forms to be discriminated were a circle and an ellipse. At first an ellipse was used, the ratio of whose semi-axes was as 2:1. The discrimination was apparently made. This was followed by using a series of ellipses gradually approximating the circle in form. The ellipse whose semi-axes bore the ratio 9:8 proved to be the limit at which differentiation just failed. Returning to the flatter and longer ellipse, and reestablishing the discrimination for it, the threshold was again approached and with the same result. The indication is therefore for an acuity not far inferior to that of man. This conclusion is, however, not supported by any other modern work from the Pavlov laboratory so far as we know, and is, furthermore, contrary to the bulk of evidence from all other sources.

Can the dog see colors or is his visual world composed of only lighter and darker shades? The general opinion of animal psychologists, in the light of tests made on various forms, is that no mammal below the monkeys and apes is capable of color discrimination.

No study of color vision in the dog has been made by means of the Yerkes-Watson method described above. So far as the writers are aware the latest investigation in this field is that of Smith (44) published in 1912. Experimentation on color-vision in dogs has been, almost without exception, of the crudest sort. Even the experimenter has not been eliminated from the situation. Prismatic colors have never been employed. Usu-

ally light reflected from colored pieces of paper, painted food containers, colored balls, and the like has been utilized. Control of the intensity factor has never been adequate and in many cases has been quite overlooked. The results reported, and they are about equally divided for and against the existence of color vision in dogs, therefore cannot be taken seriously. Perhaps the least inadequate study making use of reflected rather than transmitted light, is that of Smith. This writer has been generally quoted as having concluded in favor of color vision (see Washburn, Animal Mind, p. 156). A careful reading of his paper shows that this does not fairly represent his position and that the data he presents certainly support no such conclusion. Although Smith is inclined to suppose that certain dogs may be able to discriminate colors to a limited extent, he emphasizes his opinion that such discrimination "is highly unstable and cannot be supposed to play any part in the animal's normal existence." For all practical purposes this is equivalent to a denial of color vision. This tentative conclusion is quite in agreement with the work of the Russian school, as is indicated by the following quotation from Pavlov (35, page 132 f.): "Dr. Orbeli in a first series of experiments was unable to detect any differentiation of colours on the part of his dogs. In a second series of experiments, however, positive results were obtained in one dog, but only with great difficulty, and even in this case the experiments were still open to criticism. The results obtained by other investigators, both Russian and foreign, lead to the conclusion that colour vision in dogs, if present, is only of a very rudimentary form, and that in most dogs it cannot be detected at all."

It must be concluded, therefore, on the basis of laboratory tests that the dog's vision is decidedly inferior. The casual observations made at home and in the field do not conflict with this conclusion. In the every day life of the dog it is no doubt a supplementary sense, rather than the dominant sense as in man. In the laboratory it seems called into play only when the more dominant senses, the olfactory and the kinesthetic, fail to bring the animal success. The discrimination experiments already reported are examples, and there are others which even more clearly indicate the tendency of the animal to overlook visual clues in favor of those of other modalities. This conclusion applies only to still and not necessarily to moving objects. De Jong (24), after training his dogs to open a box by lifting a latch in order to obtain food, turned the box ninety degrees, in the dog's absence. The dogs then went to the point on the box where the latch had previously been and made the movement of the paw that had formerly served to lift the latch. This of course failed to produce the desired results, but the dog nevertheless continued to attack that same point for some time, entirely overlooking the rather prominent latch, which, although at a new place, was still clearly within his visual range. Learning to open the door with the box so turned seemed to be an entirely new problem, accomplished in the usual trial and error manner. Only after the position of the box had been shifted a number of times, and relearned as often, did the dogs finally come to respond to the latch itself, and even then not necessarily on the basis of vision alone. Experiments similar to these have been made by Johnson (20) with similar results. An even more striking demonstration of the insignificant rôle of eyesight is found in other of Johnson's experiments. He found that problem boxes were solved as readily by dogs temporarily deprived of

the use of vision as by their normal companions and, furthermore, that normal dogs worked in the dark almost as efficiently as in the daylight. Hamilton (13), Buytendijk and Hage (5), and others have attempted to facilitate the solution of problems by introducing prominent visual cues, which one would expect to be of real aid to the dogs, with but little or no effect.

Although there is little experimental evidence on the subject of moving versus still objects as visual stimuli, such as there is agrees with casual observations of a number of investigators to the effect that the dog is extremely sensitive to objects in motion. A preliminary study of the subject has been made in the laboratory of Pavlov, but no limits of discrimination have been determined.

Interesting indication of the great sensitivity of the dog to slight movements is to be found in the several examples of the Clever Hans error—an error which is as likely to occur in the study of dogs as in the case of the famous horse after which it was named. It seems probable that the cues imperceptible to us which the animal gets from the experimenter are chiefly visual, although audition may be involved here also. In the early experiments on auditory discrimination made by Kalischer (25), Rothmann (37), Swift (47 and 48), and others it seems very probable that the dogs obtained secondary cues from the experimenter, who was always present. Swift, for example, seems to give his case away in the following statement (48): "I found at first he (the dog) was inclined to react to motion rather than sound, and watched me closely for the motion accompanying the low tone, and would react to that." According to the conditions of the experiment the dog was allowed to take food from the experimenter's hand when this low tone was sounded. In spite of the above-quoted statement that the dog appeared at first to react to slight movements of the experimenter no effort seems to have been made to eliminate the experimenter in this case, and the writer goes on to assume the problem to have been learned on the basis of auditory cues. Johnson, studying the same problem (20), apparently had evidence for pitch discrimination in the earlier part of his work, during which the experimenter was present, but when the conditions were so modified that the experimenter was entirely concealed the discrimination could not be made. This indicates rather conclusively that the dog had been reacting not to sounds, but to slight movements made by the experimenter.

Olfactory capacity

The dog is popularly accredited with the possession of a remarkably efficient nose. It is through his superiority to man with respect to olfactory acuity that he has most frequently been of practical service to his master. He has been used to trail and retrieve game, to find lost articles and people, to detect fleeing and hiding fugitives from justice. Very little strictly laboratory work on the subject has been reported. None such has appeared from laboratories in this country. No doubt the chief reason for the paucity of work on olfaction, not only in dogs but in almost all animal forms, lies in the recognition by investigators of the great difficulty of controlling the stimuli in question.

An instance of the dog's olfactory acuity and, incidentally, an illustration of the difficulty of animal experimentation, is to be found in an early study of Johnson's (22). This careful investigator, while studying visual acuity in an English bull terrier, obtained such a fine degree of visual discrimination as to render him

incredulous. One by one he checked over the possible secondary criteria which might be giving the animal the clue for its choices. He was using an electric grid to punish wrong choices (in addition to a food reward), and it occurred to him that the animal might in some way be able to detect which of the two grids was electrified in a given trial. He therefore ran a control series with both grids electrified, cutting off the current on the side of correct choice only after the choice was made. The habit broke down immediately, the animal now responding quite by chance to the right or left side. It seemed that the difference in potential between the charged electrodes had caused a release of ozone, in minute quantities, but evidently sufficient to be the basis of the discriminating behavior.

The first question we should try to answer relates to the kinds of odors to which dogs will respond. Binet and Passy (2) claim that dogs respond to animal odors but not to odors arising from vegetable matter. Heitzenroeder (15) using a Spitz obtained evidence leading him to the conclusion that the threshold for odorous mixtures of animal origin was far lower in the dog than in man but that the threshold for odors of plants and perfume was lower in man than in the dog. His method was that of introducing the air carrying the odor by means of a funnel-like arrangement over the dog's nose and taking as indication of sensitivity a sniffing movement or change in the breathing rate. That lack of such overt response would indicate lack of sensitivity is to be seriously doubted. Seffrin (39) used Heitzenroeder's method and reached similar conclusions. Henning (16) recognizes three possible explanations: (1) the olfactory continuum shows prominent gaps or breaks; (2) all odors are sensed, but some types have a disproportionately high threshold; (3) such motor responses as sniffing are given, normally, only to biologically important odors. Henning apparently felt that the last possibility was most likely the true one, for in his study he used a different form of response. Henning's principal method involved the use of nine handkerchiefs scattered on the floor of an empty room. One of these was saturated with a definite odor. In an adjoining room the dog was given the opportunity of smelling the odor in question and was then sent into the test room to retrieve the scented handkerchief. The position of this handkerchief was varied from trial to trial. A Dobermann and a fox terrier are said to have retrieved without error the correct handkerchief when the following odors were used in intensities equalling the human threshold (subjectively determined): vanillin, heliotropin, cumarin, oil of rose, oil of geranium, jasmine, oil of lemon, peppermint, wintergreen, and others. A greyhound could not be trained to do this. This test gave no evidence of discriminatory ability but only of sensitivity, since only one odor was used at a time. Further tests of a rather informal nature indicated that the dogs could discriminate between food odors and flower odors.

Buytendijk (4) presents data not only on the lower threshold but on discriminatory ability. He employed two methods, principally. In the first of these, two boxes were used, exactly similar and each containing a biscuit. The lid of one was fastened shut, while that of the other could be opened. A small vessel containing a chemical, diluted in paraffin or water, stood before each box, and it was supposedly only by detecting the odors that the dog could tell which box was unlocked. Buytendijk apparently did not take care to eliminate the experimenter from the situation, and we cannot be sure

that the animal was not responding to some cue from himself. The results reported seem to indicate that the smells of nitro-benzol and benzaldehyd, which man cannot distinguish, are also confused by the dog. On the other hand, 0.01 per cent nitro-benzol was analyzed out of a mixture of 0.1 per cent each of eugenal, ionon, linalool, and zimtaldehyd. A number of other mixtures were also successfully analyzed. As to absolute threshholds, vinegar was distinguished in a dilution of $1:10^6$, salt and vinegar acids in dilutions of $1:10^5$, salt and quinine in dilutions of $1:10^4$. Buytendijk's second method made use of glass dishes which contained the odorous substances each held in a sort of basket with a handle permitting the dog to pick them up singly and retrieve them. The procedure was essentially that used by Henning with the handkerchiefs, except that but three receptacles were used at a time. Solutions of formic and of sulphuric acid containing one part in ten million were correctly responded to, as were also extremely dilute solutions of a number of other acids. All such solutions were said to be quite odorless to man. Here again there exists the possibility that the dog reacted to cues given by the experimenter.

To what practical use can the dog put his olfactory ability? In the first place it is so generally accepted that certain dogs are able to follow the trails of other animals that special tests of this ability have apparently seemed unnecessary. This does not mean, however, that a dog can distinguish between the trail of animal *x* and animal *y* of the same species nor, perhaps, that he can distinguish between the trails of individuals of closely related species, although most hunters will say that dogs readily do so. Bingham (3) reports that a setter who normally pointed birds very skillfully had on occasions followed trails which proved to have been made by turtles, and he states that other cases of this sort have been brought to his attention. It seems probable that olfactory reception is dominantly if not solely responsible for much trailing behavior. That trails are followed more readily when they have been recently made is doubtless due to the fact that the odorous particles, emanating most probably from the footprint of the trailed animal, diffuse rapidly and finally reach a degree of dilution such as to render them below the lower threshold of the dog. Tests made by Buytendijk on a German Shepherd dog (4) indicate, among other things, the effect of wind on the trail. When following a trail leading straight into the wind, or when following a trail behind an obstruction which cut off the wind the dog followed almost exactly the steps of the man being trailed. But when the trail crossed open country at right angles to the wind the dog did not follow exactly the path of the man but ran along rather uniformly from one to two meters or more to the leeward of this path.

Although Romanes' tests of the sense of smell in his female setter (36) have frequently been referred to, certain interesting details have been overlooked. It will be remembered that this animal could trail Romanes successfully even though a number of people were made to walk single file behind him in such a way as apparently to obliterate his trail. By appropriate tests Romanes found that the dog would not follow his trail when he was barefoot, in stocking feet, or wearing a pair of new boots, that the dog would follow the trail of a stranger only if that stranger wore a pair of Romanes' old boots. It was apparently the old boots which were being trailed. Romanes then proceeded to paste heavy brown paper en-

tirely over his boots, soles and all. The dog was unable to trail him when he wore his boots so covered. After walking some distance a small bit of the paper wore off the heel of one of the boots. When the dog, which had been led along the trail far behind in the meantime, reached the point where the heel had worn through and was thus making contact with the ground it picked up the trail at once and soon caught up with Romanes. This little incident hints at the extreme delicacy of the stimulus which is apparently effective in trailing behavior. A characteristic of trailing which has never been adequately explained, as Johnson has pointed out (21), is that a dog when coming upon a trail at right angles seems able to detect almost at once the direction taken by the animal or man making the trail. It seems impossible to imagine what the cue can be to such behavior.

Romanes' dog could apparently discriminate by odor his boots from other boots. A more thoroughgoing test of the ability of a dog to select objects belonging to a specific individual has recently been made by Löhner (28). In this case not trailing, but retrieving was the behavior employed to demonstrate the ability to distinguish between the odor traces left by various individuals. But one subject, a two year old female German Shepherd dog, was used, and in every case the object to be retrieved was one which had been handled by her keeper. The objects in question were small pieces of pine wood. One of these was just held in the keeper's hand, and then placed, with forceps, with ten to twenty other pieces which had not been so handled. The dog was allowed to sniff her keeper's hand and was then told to get his piece of wood. She was successful in every case. An attempt was made to discover to what extent it was necessary to handle the pieces. Apparently the shortest duration necessary to their identification was 2 seconds and the smallest surface was that touched by the finger tip. Washing the hands of the keeper in alcohol before touching the wood did not interfere with the identification. Even though four or five pieces of wood handled by others than her keeper were introduced among the dummy pieces, the dog appeared able to select her keeper's piece. At no time was the dog asked to retrieve pieces held by anyone but her keeper. Apparently these experiments were conducted extremely carefully, but, unfortunately, it is not stated whether or not the keeper, or other observers with knowledge of the correct object, were within the visual range of the dog during the selection. If this was the case (and mention would probably have been made of it were it not) the results could scarcely be accepted.

It may be, however, that a dog is capable not only of following human and animal trails but of selecting objects which belong to, or have been handled by its master. Whether this ability to identify the odor traces of an individual person extends to other than the dog's own master has not been established. Nor has it been proven that, upon being given the hat or some other article belonging to a stranger, the dog can select that stranger from among a group of persons. In spite of the fact that the dog's ability along these lines is not definitely known, evidence which depends directly upon such ability is admitted by the courts of many states of this country and also in certain foreign lands. Much more of the validity of such evidence should be known if convictions are to be made on the basis thereof. Realizing this, certain German police officials, notably Police Lieutenant K. Most, with the cooperation of Professor Pfungst conducted a series of tests a

few years ago, in Berlin. These are reported by Craig (7), who, however, fails to give the original reference. The tests were open not only to police dogs but to all comers, and retests were permitted after failures when so desired. A number of prize winning dogs of various breeds were entered and tested individually. Four types of test were given. The first involved the following of a fresh human trail among other recently made trails. No dog proved able to do this reliably, although most were able to follow a fresh trail over older trails. Among fresh trails the dogs often switched from one to another, the angles of intersection seeming to play a prominent part in determining which trail was to be followed. The tendency was for the dog to follow any fresh trail extending in the same general direction taken by the trail he had just been following, i.e. if the trail he was following in a northerly direction turned abruptly east, at a point where it intersected a second fresh trail which from that point extended northerly, the dog usually followed the second trail.

The second test involved the following of an old trail over ground entirely free from other trails. Twenty tests over trails from $5\frac{1}{2}$ to $6\frac{1}{2}$ hours old resulted in absolute failure. Trails were followed well only when not more than 30 minutes old.

The third test involved the selection from a group of objects of the one previously handled by a person who had been pointed out to the dog. In other words, this corresponds to Löhner's experiment except that other individuals than the dog's master were used. In no case did a dog make a correct choice more often than he might have by chance.

The last test was the converse of the previous one. The dog was given the glove of a person and told to select the owner, who, together with nine other men, stood in line with their backs to the dog. In no case did the men know whose glove had been given the dog to smell. This precaution prevented the "guilty" man from revealing his identity in any way. The dogs all failed in this test as completely as in the previous ones.

The conclusions drawn were that those cases of successful detection of criminals by dogs (as demonstrated by subsequent confessions) were probably made on the basis of slight movements of the criminal resulting from his fear of being detected. Those cases where a dog had apparently trailed a criminal to his lair were interpreted as examples of the Clever Hans error. It was supposed that the police sergeant holding the leash on which the dog was led while trailing often had a sagacious guess as to the probable hiding place of the criminal and, all unwittingly, led the dog to that place, rather than being led by the dog. In other words it was a case similar to the "muscle-reading" by which so-called mind-readers often successfully entertain parlor audiences. As a result of such tests, so Craig reports, the use of dogs in criminal detection is now forbidden by the Prussian government.

How are we to interpret these results? It seems to the writers that these negative results cannot be taken as definitely proving a lower degree of olfactory acuity in dogs than had previously been granted them. It is more probable, in view of the other evidence in favor of extraordinary acuity, that these tests indicate that the problems were not properly set for the dogs. To use, for the sake of simplicity, an anthropomorphic term, we have no evidence that the dogs understood what was expected of them. Negative conclusions are always difficult to support, and they are certainly not justified in the absence of evidence that the problem at

hand has been adequately set and that sufficient motivation has been brought to bear upon its solution.

We are not at all inclined to belittle the dog's olfactory acuity and feel that the bulk of the evidence shows it to be far superior to our own.

Auditory capacity

Experimental evidence on hearing in dogs appears to indicate that they are at least as sensitive as man in this respect, while their capacity for auditory discrimination is less certainly known.

Only one study of intensity discrimination has been made, that by Tihomirov, a student of Pavlov. He used an organ pipe with an arrangement for damping the sound as desired. The results seem too good to be true and are perhaps best covered by quoting from Pavlov (35, p. 135): " . . . it was found that an intensity very closely approaching the one employed as a positive conditioned stimulus could be differentiated by the dog with an absolute precision even when a pause of 17 hours was made between the two stimuli. The experimenter found himself able to detect a difference between these two intensities of the sound only when they succeeded each other immediately. . . . In the continuation of these experiments the intensity of the inhibitory tone was brought still nearer to the intensity used for the positive conditioned stimulus, and an absolute differentiation was obtained even after a pause of three hours between the stimuli. Unfortunately these experiments were conducted in our old laboratory where the effect of the inhibitory stimulus was easily disturbed, and it must be left to the future to repeat these experiments under more perfect conditions in our new laboratory."

The bulk of the experiments on pitch discrimination leave much to be desired in the way of technique. The experimenter has usually been present, and pure tones have seldom if ever been used. All investigators but Johnson have found some degree of pitch discrimination. Johnson's work was inspired by reports of some of the earlier work done in Pavlov's laboratory (by Selionyi and by Beliakov) in which it was claimed that dogs could discriminate differences of one quarter and even one eighth of a tone. Johnson justly criticizes this work in the article reporting his own results (20). He used the Yerkes-Watson discrimination apparatus employing both punishment and reward. The experimenter was eliminated. The sounds were produced by electrically driven tuning forks. To one note the dog was required to turn to the right to be rewarded, to the other he was required to turn to the left. Although the dogs were given a prolonged training series there was no evidence that they could learn to make the discrimination. Pavlov set Anrep on the problem of repeating the earlier work of Selionyi, which had not been accepted by American investigators. Anrep (1) criticizes Johnson's work on two grounds. The first criticism is methodological. It is his opinion that the problem as set by Johnson is far too complicated. The animal is rewarded for both sounds, although at different places and, similarly, when it makes a wrong choice it is punished while both sounds are being given. We are forced to agree that the Pavlov method presents the animal with a far simpler learning problem. The one note is continually reenforced by food, the other note is never so reenforced.

Anrep's second criticism relates to the production of the tones, it being his claim that it is impossible to eliminate entirely the noise of the "make and break" when using electrically driven

tuning forks. Anrep used electric resonances and a synchronous motor, driven by alternating current producing, supposedly, a sinusoidal curve. As a sound generator in the experimental room a pair of telephones was used. These were placed close together, each attuned to the pitch which it was to transmit. Anrep reports discrimination in the case of one dog of two notes differing but slightly in pitch, the one 637.5 d.v. and the other 680. d.v.

The controversy regarding pitch discrimination in the dog can only be settled by further work.

The only data on the upper limit of the auditory range in the dog come from the Leningrad laboratory (Bourmakin, Andréev). These indicate a sensitivity to sounds far above the highest note audible to man, or up to 100,000 d.v. Other work by Pavlov's students indicates remarkable discriminatory ability for notes alike in pitch but differing in timbre or tone color, and also extreme sensitivity to differences in the periodicity of the beating of a metronome.

That the dog is able to localize the source of sounds with reasonable accuracy has been demonstrated by Johnson (20) although he did not study the limits of their sensitivity in this respect.

Regarding the ability of the dog to respond to the human voice there is a wealth of anecdote but a paucity of experimentation. There is, of course, no question but that they can hear spoken words, but as to the number of spoken words that can be discriminated by a given trained dog there is very little evidence. It has been proven in the case of certain dogs who have been supposed to give differential response to a large number of words that they were merely following a routine, that if the commands were given in an altered order the dog would respond as though the original order had been repeated. Don, the talking dog, is the classic example of response to routine (19). A bull terrier, Jasper by name, was claimed by its owner to have an understanding of several hundred words. No thoroughgoing tests were made of the dog, but Watson was inclined, as a result of observations of his behavior, to consider such a claim far too extravagant. (55, page 315).

Edinger (9) trained a female Shepherd dog to respond appropriately to a number of simple commands. She could turn the knob of a door and open it. She could also close doors but often confused the two responses, turning the knob of an open door, and so on. If she was told to close a door which was swung open *away* from her she was quite helpless, not making the response obvious to us of going around behind the door and pushing it shut. Edinger believes that the responses were not given to the spoken commands as words, since nonsense words served just as well if corresponding inflections were maintained. Schiche (40), on the other hand, believes dogs to be capable of a rather fine degree of discrimination of consonants. He trained police dogs to sit at the command of "Setz" and to lie down at the command, "Platz." To such similarly sounding syllables as "seck," "retz," "petz," and "ketz" the dogs did not react. We judge, however, that the experimenter was always present.

Perhaps the dog for whom the most astounding performances have been claimed is the Airedale, Rolf, often referred to as the dog of Mannheim (27, 30). This dog was usually present during the daily lessons of some young children. One day while chastizing the children for failing on some simple arithmetical problem the tutor remarked that the problem was so simple that even Rolf

could solve it. Thereupon Rolf proved himself worthy of such opinion by tapping out the proper answer with his paw. This led to a systematic education of the dog involving not merely the simpler arithmetical problems but also square roots and so on. The dog also learned to spell, using taps of the paw to represent letters. It is said that at the suggestion of his mistress he manufactured his own alphabetical system, and it is claimed by his proud owners that, apparently in the interests of efficiency, this system involved the fewest number of taps for those letters which are ordinarily used most frequently. It is difficult to evaluate the so-called tests made of this dog because of their uncritical nature. Every opportunity was given for the operation of the Clever Hans error. Only one incident reported cannot readily be explained on that basis. In this case the cards, on which the problem given the dog was presented, were shuffled by the observers and shown the dog at random and without any of the observers knowing just which card had been presented, and thus what reply to expect. Unfortunately these conditions were not maintained often enough to yield results of statistical validity. The attention of Claparède, one of the scientists to test the horses of Elberfeld, was called to the dog, and he planned to subject him to critical tests. Probably the most brilliant thing Rolf ever did was to be taken suddenly ill soon after Professor Claparède's arrival.

Other modalities

Of the other sensory modalities little can be said, since there are at present no data upon which we might base an estimate of sensitivity and threshold values. That kinesthetic stimulation is highly important has already been suggested in connection with our consideration of the rôle of vision. It apparently dominates visual stimulation in determining the behavior of the dog under ordinary conditions. Beyond the fact that dog and man are sensitive to the same general types of tactual, thermal, gustatory, and electric stimuli little is known. To summarize: it seems probable that the average dog is far more sensitive to odors than is man; that he is not strikingly unlike man with respect to sensitivity to sounds; that his vision for still objects is decidedly inferior to that of man, while his acuity with respect to moving objects is great, although there is not sufficient data to warrant a comparison with man in this respect.

Learning ability

The learning ability of dogs has been tested by means of the usual laboratory methods. Dogs have been used by Thorndike (53), Johnson (20), and others on the problem box, by Szymanski (49) in the maze, by Hamilton (14) in a quadruple choice device, by Hunter (18) and by Walton (54) on the delayed reaction set-up and by Shepherd (41) in situations involving the pulling of a string to draw food into their reach. Apparently they have yet to be tested by the Yerkes multiple choice method. One gets a clearer impression of the dog's learning ability not by perusal of the quantitative results but by a comparison of these results with those obtained on other animals.

Without going into detail it may be said that as tested on such devices the dog appears to be superior to the cat, slightly inferior, perhaps, to the raccoon, and probably inferior to monkeys and apes. This last conclusion is, however, based only upon tests which are much more suited to the motor equipment of the monkeys and apes. Even though a dog and a monkey might be equal in intelli-

gence we should expect the latter to be more adept in the manipulation of knobs, sticks, strings, and the like, because of his well developed hand. Perhaps if monkeys and dogs were tested on a similar maze, where the responses involve only locomotion, the standing of the two forms would be reversed. We have no way of knowing, however, for this has not been done. Similarly, the only demonstration of the raccoon's superiority to the dog has been on a problem box involving manual manipulation. The raccoon's forepaw is modified so as to be fairly efficient in grasping articles. The dog's paw is, of course, ill suited for such uses and, as a matter of fact, a dog often prefers to use his mouth. Dogs have shown very little ability to imitate each other or man, but this lack does not place them below other animals, since experimentation has shown that true imitation is rarely found in any animal form, even among the higher apes.

A few words on the dog as a psychological subject may not be out of place. As is well known the rodents are represented in behavior studies by the white rat. The selection of a single representative species upon which all experimenters interested in the lower mammals should do systematic work is, of course, a great advantage, since it renders possible the collation and comparison of a vast amount of data. If some workers used squirrels, others guinea-pigs, others weasels and so on, this valuable intercomparison would scarcely be possible. Among the Carnivora there has not been such a definite concentration upon a single form, although the dog has been the chief object of study. There are a number of reasons why the dog would seem to be the logical animal to represent this group. In the first place more is already known of his sensory and learning capacities than of those of the cat, the raccoon, the porcupine, or any of the other animals of this group which have been subjected to experimentation. In the second place less interference by emotional disturbance is encountered in the case of the dog than in animals not so able to adapt themselves to the necessary experimental situation. That the emotional status of the animal during testing is highly important and should be kept as constant as possible does not seem to be sufficiently recognized. This is especially true of the higher, more complex forms. We cannot blame pioneers for having tested animals under conditions rendering them more or less frantic with hunger and fear. But it seems surprising that such a recent worker as Williams (56) should take seriously his negative results on form discrimination in dogs when his subjects were, judging from his descriptions, highly nervous and fearful during the tests. To quote: " . . . . a dog occasionally develops the obsession that he can not get out of the blind alley and stands yelping, enduring for a time the punishment (electric shock). In such a situation it may be necessary to move up the secondary coil thus making the electric current stronger till it is of sufficient intensity to overcome the obsession and force the dog to become more diligent in search of a way out." Williams used punishment only. To quote again: "With the method of punishment by electric shocks, little time need be wasted, if all parts of the apparatus are in good working order, as the animal can be forced by the shocks to move to any part of the apparatus at the will of the operator." No doubt such an investigator would consider it a waste of time to become sufficiently *en rapport* with the dog to permit the use of the normally strong desire of a dog to please his master as motivation.

This brings us to the third qualification of the dog which renders it capable of becoming an ideal laboratory subject. The dog is unquestionably more sensitive to the whims of a man who has won his confidence than is any other carnivore, or perhaps any other infra-human animal, for that matter. The cat, for example, is scarcely at all dominated by man, except in his rôle as provider. Thus starving or using some such punishment as electric shock is practically necessary to produce sufficient motivation to insure their attacking laboratory problems. Even in monkeys and apes the problem of motivation is a difficult one if we may judge from reports in the literature. The dog has continually demonstrated his ability to adapt himself readily to the wide variety of conditions which man has imposed upon him. He has cooperated with man in war and in peace, in the forests, in pastures, and in the city. Nor has he failed to cooperate even in the psychological laboratory except when no effort has been made to deal with him in a manner befitting his high degree of complexity and sensitivity. Many examples might be given to show his willingness to play his part in experimental situations in the absence of harsh forms of motivation. The dogs used in the Leningrad laboratory are said to jump up onto the experimental tables without command and to lift up their feet one at a time to permit the adjustment of the necessary harness. An early study of Hamilton's on a young bull terrier (14) gives an admirable instance of adjustment to an experimental situation. The problem presented to the dog was an extremely difficult one, that of releasing himself from a box by the manipulation of a system of pedals. This dog worked daily on the problem over a period of many weeks with, apparently, unflagging zeal even though no punishment was used and the reward consisted not of food but only of petting and a few kind words. It seems only reasonable to suppose that an animal working under natural and undisturbing conditions would be more nearly capable of giving a performance record, whether of discrimination or of learning, that would represent its maximum capacity than would an animal working under the stress of punishment or too severe hunger. The dog is one of the few animals which will work without such motivation.

One of the reasons for the discrepancies that exist among experimenters on the dog's capacities is no doubt the fact that all sizes and sorts of dogs have been used from highly bred bull terriers to an assortment of mongrels. It would no doubt be well to settle upon a representative breed for systematic experimentation, but the writers are at present in no position to make a definite proposal as to which of the many breeds is best suited to the purpose.

II. RECENT TESTS OF THE ABILITY OF "FELLOW" TO RESPOND TO VERBAL STIMULI (OR TO UNDERSTAND HUMAN LANGUAGE)

Fellow is a thoroughbred German Shepherd male, between 4 and 5 years of age, with a long line of famous blooded ancestry behind him, and owned by Mr. Jacob Herbert of Detroit, Michigan. Mr. Herbert has made a hobby of fine dogs for years and selected Fellow from among scores that he has bred, and sought to teach him in various ways to understand human language in the sense of responding in the appropriate manner to commands. This type of training is, of course, not especially new. The verbal cue has been often employed in professionally trained animals, and everyone has taught his dog to do, upon proper command, a few tricks at least. But Fellow, as Mr. Herbert

explains, has been talked to constantly almost from birth in much the same manner as a young child during the years of taking on language, and it was this fact of the extensiveness of such experience and its possible effect upon the dog that made his case particularly interesting. Mr. Herbert believes that Fellow has picked up from this long contact with mankind some four hundred or more words, and that he understands these words in much the same manner as a child under the same circumstances would. By the term "understanding" Mr. Herbert seems to mean no more than that definite associations have been formed between specific words on the one hand and specific objects, places or acts on the other. As a layman he has no opinion to offer regarding any so-called mental or subjective content of the dog's mind in connection with these words, claiming only that the words operate in some manner as the essential signals in determining the dog's behavior. From conversation with him we gather that he doubts the ability of the dog to recall the words voluntarily, in a manner supposedly characteristic of human thought processes, and thinks of the dog as being capable of merely recognizing or identifying the object, place, or act when the word is spoken in the presence of the corresponding thing or event. He does not consider the facts in the case to offer any positive evidence of reasoning in the more technical sense.

Our personal acquaintance with both the dog and his owner began on September 29 last when we went to the Pasadena Hotel, New York City, at the request of Mr. Herbert to witness the performance of Fellow and to make such tests as we might see fit. Mr. Herbert was anxious to have his opinion of the dog's ability checked up by psychologists.

Aside from the matter of responding to words, no special claims were made for the dog. As his master explained, Fellow was not a trick dog—had not been trained to perform any unusual stunts. He had quite successfully played, indeed, the usual rôles allotted to his species in movie-melodrama—those of protecting the helpless and saving the drowning child, had starred in "Chief of the Pack" and other animal cinemas, but no special effort had been made to develop in him unusual motor performance. His claim to special attention lay in his accomplishment of responding to a large number of human words in some sense or other, and the problem before us was to determine in precisely what sense.

Mr. Herbert recognized the possibility of error in a layman's opinion regarding the ability of Fellow along linguistic lines and received us in a questioning rather than an argumentative mood. From the first he showed every willingness to cooperate with us in an honest effort to discover the facts in the case. In truth, Mr. Herbert deserves great credit for the straightforward attitude which he has maintained throughout the tests, regardless of their effect on his own personal opinions concerning the ability of his companion and friend. He has not sought to explain away failure in certain cases by insisting that the tests were unfair, the dog indisposed or tired, or by any of the escape mechanisms often employed by professional trainers to preserve the reputation of their protegé, or their own personal illusions of special or mysterious genius. That the owner of the dog was thus able to enter into the scientific spirit of the enterprise and give us a free rein in testing the dog had much to do with whatever success has attended our efforts.

Our first examination of Fellow was strictly private, only one person being

present in addition to Mr. Herbert and the writers. We watched the dog perform for half an hour or so—remarkably well it seemed to us in spite of our chronic skeptical attitude. We noted that no attempt was made by the owner to use identical phrases in the commands covering the same preformance, nor was any set order followed in the performances. The commands were given in a natural conversational tone as if the owner were holding a conversation with the dog. We were quite convinced before the examination was over that the performance of the dog was far above the level of routine so characteristic of the usual animal trained for purposes of exhibition. Even when we, ourselves, determined the order of the commands in a hit and miss manner the performance was perfect. Our opinion that the different acts were quite isolated from one another and involved no element of routine whatsoever has been fully borne out by all later tests.

The problem as to the nature of the stimulus cues determining the responses of the dog could not, of course, be so easily disposed of. The first point to settle was whether the essential stimuli were actually auditory or not. For after all the dog might be depending upon unintentional gesture, or other visual cue so long as he performed always in the presence of his master. The possibility of the "Clever Hans" error must be effectually ruled out in view of the fact that Johnson (20) had found it to be a complicating factor in his work on auditory sensitivity in dogs. Certain pitch discrimination habits, or what seemed to be such, broke down entirely when the experimenter absented himself from the room during the experiment.

In the absence of a screen, Mr. Herbert was stationed in the bathroom of the suite and gave his commands through the closed door while the writers remained in the room with the dog to observe and to give the necessary signals for the successive commands. We were very careful not to aid Fellow in any way by movements of body, head or eye. Although not perfect, the dog's performance was on the whole quite satisfactory, and especially so in view of the fact that the arrangement of having the master absent was entirely new, and the commands were noticeably less audible. It was evident that visual cues from Mr. Herbert were quite unnecessary to successful response in many cases at least, the essential stimuli being auditory in character.

It would have been desirable to run a series of control tests to determine more precisely the nature of the auditory cues and particularly what, if any, language elements were involved. We were handicapped at this point, however, by the fact that Fellow is a one-man dog and has been trained not to respond to the commands of others than his master. Such training is perhaps necessary if an animal is to play his part well on the stage or in a cinema rôle. It was impossible to carry out our original intention, therefore, of making systematic tests in which the commands should be given by other persons with varying pitch and different intonation. We had thought of introducing a woman's voice in this connection. We did find that Fellow would obey the commands of persons with whom he has been associated for some time, after getting a nod of approval from his master. Furthermore, Mr. Herbert varied his own voice in pitch, intensity and intonation—sometimes giving the commands in a monotone—without disturbing the dog's performance.

It was evident that the dog has associated certain sounds, of the human, verbal pattern type, with definite responses, but

was this equivalent to understanding words in the human sense? The question as to whether a spoken word is a true language element, or merely an auditory stimulation of the non-language type, is after all a highly technical one, and depends in the last analysis upon an acceptable definition of an elementary language element. So far as the present writers know a satisfactory distinction on this point has not as yet been made. If we define too strictly, many responses of the human that we ordinarily think of as language are probably not really such, whereas a broader definition of the term might easily overthrow the distinction entirely. Perhaps we are here faced with the usual difficulty of scientific classification, where genuinely discrete elements are not involved but only differences in degree. May it not be that here as in most cases we have not distinct classes of stimuli—language vs. non-language—but a graded series of stimulus situations in which the application of arbitrary classificatory criteria is almost worthless, if not absolutely misleading? The problem is not strictly confined, moreover, to studies of auditory responses in infrahuman forms. In the human infant and young child it bobs up again and again to disturb the human psychologist. A genetic account of the development of language in the child would undoubtedly throw much light on our own problem. Perhaps it would be found that in this case words are responded to at first as purely auditory stimuli, and as development proceeds these sounds take on more and more of the attributes which we have come to associate in our thinking with language in the more exact sense.

As a result of the completion of this first examination of the dog we issued the following statement to the press in order to avoid the usual scandal of newspaper accounts. That we were not able wholly to escape will be seen when this statement is compared with the headlines that have appeared both at home and abroad in connection with the test.

> We have just completed a test of an hour and a half on "Fellow," the famous movie-actor dog and it is a most remarkable dog in many respects. It is certain that the dog obeys commands given by the human voice with remarkable speed and facility. The commands do not need to be given in any set order as the dog has been taught so well that a routine line of command and performance is not at all necessary. This is the more surprising in view of the fact that no punishment has been used in training the animal—he has been given much the same treatment by Mr. Herbert as one would give a child.
>
> One point is definitely settled—the dog does not require gesture in addition to the human voice, at least in many of its performances. Mr. Herbert gave commands from an adjoining room with the door closed, and with no one but total strangers in the room with the dog. The animal would go to the window, go into another room and do various things, pick out objects from among several, etc., when the commands were given from the room in which Mr. Herbert was concealed.
>
> One point remains to be settled, if indeed it can be settled at the present state of our knowledge of animal behavior. That is, does the dog understand words in the human sense? This is a difficult point to settle inasmuch as it is possible for an animal to obey commands to words, not as words but as sounds. Such tests as were made, that of changing the tone in which the commands were given and of giving confusion commands still leave the matter in doubt. Personally we are of the opinion that the dog has learned to associate certain sounds, rather than words in the human sense, with the proper objects and commands. However, the large number of associations clearly mark the dog as most extraordinary.
>
> (Signed) Professor C. J. Warden and
> Dr. L. H. Warner.

It will be noted that the statement is in general conservative and contains no comparison whatsoever between the intelligence of Fellow and that of a child. Such comparisons are manifestly absurd since a common rating scale, or test applicable to both has not yet been de-

vised, if indeed it ever can be. The newspaper headliner to the effect that we had found the dog equal in intelligence to a child of six or eight years of age must have been invented by the printer's devil. Or perhaps it originated from a dullard's confusion in connection with a statement once made by Mr. Herbert that the dog understood as many words as a child of this age. The newspaper publicity began when Mr. Herbert came out to Columbia, at our request, to make a demonstration performance (not a test) before a class of graduate students in comparative psychology. The press got wind of this demonstration and attended in a body, and the next day five of the principal producers of movie news reels were on hand with their usual irresistible insistence.

Although Mr. Herbert and Fellow were very busy a short series of tests to be carried out in the psychological laboratory at Columbia was arranged. It seemed desirable to repeat the test designed to rule out the possibility of visual cues, under better controlled conditions (that is, with no one at all present during performance) and to secure data regarding the total number of words to which the dog would thus respond. Furthermore, we wished to test the ability of the dog to identify and retrieve a given object from among several upon command. The usual stage performance of Fellow is from 20 to 30 minutes whereas our test periods ranged from one to two hours, since we wished to secure as much data as possible at such times as the dog could be placed at our disposal. The use of long test periods was unfortunate inasmuch as Fellow often gave every indication of being weary of his task before the end of the longer periods, although continuing to work when duly encouraged by his master. Aside from the word "Shame" or "That's no good," spoken in a somewhat scolding tone, no punishment has ever been used either in training or testing the dog.

In re-testing the dog's ability to respond to commands in the laboratory Mr. Herbert and both experimenters were concealed behind screens so that there was no opportunity whatsoever for the Clever Hans error to enter into the results. Several chairs, tables, and such other objects as were to be used, were placed in chance locations about the room, which included also two windows and one door. The behavior of the dog was observed through a slit in the screen by one observer and recorded, while the other reported to Mr. Herbert and indicated the command to be given next. Reaction times were not taken in this series of tests. On all three days the command-performance test was given after Fellow had been working for an hour or more at the retrieving-objects test, to be described later, and naturally he was not at his best on all occasions.

It soon became apparent that certain commands could be carried out as perfectly under our test conditions as when the master was present but that others could not. After some attempt at analysis we discovered that the repertory of commands classified readily into two quite distinct groups. Type I, as listed in table 1, did not involve any very definite identification of object or place, but consisted of some movement of the animal's body in whatever place he happened to be at the moment. Type II, on the other hand, required the animal to identify and orient himself toward some object or place after the command had been given. The former response could be made immediately after the command issued, the latter usually involved a delay of considerable length. In fact, it constituted a typical delayed reaction situation except for the fact that the signal was a sound, or word instead of a light and presupposed that a

TABLE 1

Items selected from this list in command-performance test

TYPE I—NO SPECIAL ORIENTATION TO OBJECT OR POSITION REQUIRED

1. Sit (on haunches)
2. Sit down (on all fours)
3. Stand up (when sitting or lying down)
4. Stand still
5. Stand up high (against some near object, as wall etc.)
6. Step back
7. Step up closer (to object or person)
8. Roll over
9. The other way (rolls back again)
10. Turn around
11. Jump up, or get up (when sitting or lying down)
12. Jump up high (against near object or person)
13. Lay down (on haunches)
14. Lay down all the way (prostrate)
15. Lie still (when down)
16. Lay (or put) your head down (lays head down to one side)
17. On the other side (moves prostrate head to other side)
18. Turn your head
19. The other way (turns head back again)
20. Lay (or put) your head on the chair (or other object in front of him)
21. Lay (or put) your head on the lady's (or gentleman's) lap
22. Put your foot on the chair (in front of him)
23. The other foot (puts other foot on chair)
24. No, the other chair (or object or person near by)
25. Close your mouth
26. Look up high
27. Look up high at the squirrel (from watching squirrels in trees)
28. Listen to me (cocks head sidewise and looks intently at Herbert)
29. Bring the dollar (or other object in mouth or near by) to me
30. Go and take a walk (walks about slowly)
31. Go and take a run (runs to convenient spot and micturates)
32. Go and take a walk around the room
33. Go into the water (to swim)
34. Go over to the lady (or gentleman near by)
35. Stand up close to the lady (or gentleman approached)
36. Put your head up close to the lady (or gentleman approached)
37. Can anyone hurt Herbert (or other person pointed out) (barks loudly)
38. I don't trust him (barks and attacks)
39. He (she or they) is all right (ceases barking and attack)
40. Keep your eye on him (or them) (barks and attacks)
41. Careful! (ceases barking and attack)
42. Take care of him (her or them) (assumes protecting attitude)
43. Let no one touch him (her or them) (Even master cannot touch person)
44. He is a newsboy (barks and attacks)
45. There is a newsboy outside (goes to door and barks loudly)
46. Stay here, I'll be back (when leaving the apartment)
47. Speak or talk (low guttural growl)
48. Go outside and wait for me (dog leaves room and waits outside)
49. Jump up in the front (or back) seat (from other seat in car)
50. Go along with the lady (or gentleman)
51. Still (wait, stop, quit that, never mind) (stops whatever he is doing)

TABLE 1—*Continued*

52. That is all (or you can run and play now) (signal to quit work)
53. Do that once more (repeats act just done)

TYPE II—SPECIFIC ORIENTATION TO OBJECT OR POSITION REQUIRED

1. I have lost my gloves (or other object) (searches and finds object)
2. Go and get my gloves (or other object in room)
3. Go in the other room and get my gloves (or other object)
4. Go and find my keys
5. Come over to Herbert
6. Come and let me take your collar off (goes and holds out head)
7. Go and find professor (or other acquaintance)
8. Go and look out of the window
9. Now go to the other window
10. Go and put your head on the chair (table, or other object)
11. Go and jump up on the table (chair, or other appropriate object)
12. Go to the front (or back) door
13. Go and put the dollar (or other object in mouth) on the table
14. Go and find the cook
15. Come over to me and let me brush you (goes and takes proper attitude)

word-object association had previously been formed sufficiently strong to carry over the interval and lead to a recognition of the object when the latter came finally within the field of vision. The work of Hunter (18) Walton (54) and others on the delayed reaction experiment, which is relatively simple compared to the present test, should have served as a warning against expecting favorable results in this case. We know of no instance in which even the higher apes have actually demonstrated their ability to pass such a test when all visual cues have been ruled out; and of course Fellow could perform even the type II commands when his master was not behind the screen.

Without further tests we are unwilling to say that the dog cannot come up to the type II level of response, since the arrangement of hiding the master behind the screen was new and perhaps disturbing to Fellow. This may have been due, not altogether to lack of visual cues, but perhaps also to the fact that the dog was, under this condition, removed from his usual position for performing, i.e., on the stage in front of his master. Some evidence for disturbance arising from this and other conditions imposed by the test can be gathered from a close study of the detailed records.

October 30, 2:00 P.M. (all three persons present behind screens). The following commands (type II) were given along with many of the simpler sort (type I), all of the latter being correct:

1. "Jump upon the table"—Correct.
2. "Put your head on the chair"—dog jumps up on table again.
3. Command repeated twice—dog hesitates, looks toward screen, goes over to the window and looks out.
4. "Go over to the door"—dog leaves window and stands near screen.
5. "Go look out of the window"—dog jumps up on table near by.
6. "Put your head on the table"—dog looks at and approaches screen.

It was now decided to make a deliberate attempt to confuse the dog, by having Mr. Herbert come from behind the screen and issue the commands, at the same time looking away from the place or object

which the dog was supposed to approach in performing, with the following result:

1. "Go put your head on the chair"—dog jumps up on table at which Herbert is looking.
2. "Jump over the chair, good dog"—dog goes over to window at which Herbert is looking.
3. "Go over to the door"—approaches table at which Herbert is looking.
4. "Go over to the door now, I say"—goes to window slowly, toward which Herbert has turned.
5. "Go take a walk around the room"—dog goes to door at which Herbert is looking.

Mr. Herbert was then blindfolded and the test repeated to see whether Fellow got his cue from watching his master's eyes or from the general orientation of head and body. Similar results were now obtained showing that the latter factor is most likely the important one.

The dog was again tested as before with all persons present behind screens, and with similar results on November 4, and November 10. Only two commands of this order out of a total of 20 were properly executed—less indeed than pure chance should give. On their face these results seem to show that Fellow does, and must use visual cues in carrying out commands of this type. It should be pointed out, however, that not all items of the type II were tried out under test conditions and some of them would appear to be much easier than others. This point did not occur to us until we were analyzing the data a few days ago, and it was then too late to make further tests. The fact that the dog did not fail at all on the more than fifty different commands of type I, even when these were given over and over again along with the more difficult sort, shows very clearly the ability of the dog to form associations between sounds, or verbal patterns, and definite acts on his part. Furthermore, it will be seen that the dog did very well indeed on the retrieving-objects test, which happens to be the third item in our type II list, but which was tested under a more natural arrangement. We have the feeling that if Mr. Herbert would use the screen arrangement for a while in training the dog until he became accustomed to performing with his master out of sight, many if not all of the commands of type II could be carried out successfully without any visual aids whatsoever. Even in the present results, it is only the *object*, or *place* in connection with which the act is to be performed, and not the act itself that seemed to require visual cues. It is more than likely that a greater amount of practice had been given the name-act associations than the name-object, or name-place connections and hence we should expect the former to be more firmly fixed and more easily utilized.

The retrieving-objects test

According to Mr. Herbert, a large number of common objects and places are known to Fellow by name. The partial list which he gave us included the following items:

table, chair, pillow, bed, sofa, window, door, back door, front door, car, truck, elevator, water, milk, tree, wall, keys, brush, lady, gentleman, baby, boy, little boy, big boy, girl, little girl, big girl, dog, cat, puppy, shoes, baby's shoes, baby's doll, gloves, package, hat, coat, dollar (silver), money (paper), stick, ball, roof, fence, house, horse, post, lap (of person), collar, strap (leash), bite (of food), foot, head, mouth, paw, names of some 40 people and other dogs in Detroit, etc. In addition he supposedly recognizes certain terms of praise (good dog, that's fine, that's right) and certain words indicating blame (shame, that's no good).

The retrieving-objects test was designed to determine to what extent genuine name-object associations had been formed as he assumed. A number of familiar objects were placed in a room in one corner of

which an observer with stop watch was seated behind a screen. Mr. Herbert was stationed along the wall outside the room about six feet to the right of the open doorway and hence completely out of view of the objects located some 15 feet inside the room on a line with the door. The objects when retrieved were returned before the next command by a third person stationed outside the room with Mr. Herbert, who distracted the dog in the meantime by playing with him. The dog always stood outside the room facing his master when the commands were given. He must then turn about, go to the door, enter it and approach the objects lying 15 feet ahead and retrieve the proper object. The commands were often repeated but great care was taken not to repeat a command after the dog had reached the threshold of the door. This means, of course, that we have here, as in the case of all type II situations, a delayed reaction experiment and not a simple discrimination or object-recognition set-up. Inasmuch as Fellow moves about rather deliberately the interval of delay between the auditory signal (command) and the essential response (picking up the proper object) was quite considerable. The delay was never less than 5 nor more than 35 seconds and in most cases was about 15 or 20 seconds, as can be seen from table 2.

A preliminary test, October 30, in which at first ten and later five objects were employed, led to the decision to use only three objects in the test proper. A large number of objects could not be placed in the room so as to be equally accessible to the dog on approaching them, and the objects themselves naturally differed greatly in size. The low visual acuity of the dog for still objects has already been commented upon and suggests the need of ruling out any large differences in discriminability of objects in making tests of this sort. Three of the following five objects were used in each test: a man's kid glove, a seven inch scrub brush, a hotel key with tag attached, Fellow's chain collar, and a package 4 x 5 x 1 in. in size. The three objects were placed in a row about 2 feet apart and the order kept constant during each of the three test periods.

The results of this series of tests (table 2) are rather encouraging in view of the difficulty of the task. According to chance 12 of the 36 responses should be successes and 24 should be failures. Only 15 definite failures occurred as compared with 16 clear cut successes. Three of the five doubtful cases should probably be counted correct since the proper object was actually retrieved after a wrong object had first been picked up and dropped. The other two doubtful cases occurred in connection with the return by the dog of the wrong object brought on the previous trial. He failed to drop the returned object and came back with both it and the correct one in his mouth. These should probably be scored errors. On this accounting 53 per cent of the responses were correct as against an indication of $33\frac{1}{3}$ per cent by chance. The general arrangement of this test was more natural than the earlier one in which Mr. Herbert was concealed behind the screen, since the dog now came in contact with his master between trials. Fellow showed a slight tendency to bring the same object that he had brought the previous time, but this does not account for many of the errors. A more important factor was probably the relative ease with which the various objects could be picked up. Fellow has lost two teeth on one side, which interferes somewhat with the use of his mouth in retrieving objects. He appeared to avoid the package when it was lying down flat, and therefore difficult to pick up,

TABLE 2

Retrieving-object test

NUMBER OF TEST	OBJECT	COMMAND REPEATED	RESPONSE*	DELAY IN SECONDS	SCORE
			November 4, 10:45 p.m. (key with tag, collar, brush)		
1	Collar	2	n-brush, p-collar, d-collar, n-key, r-collar	20	S
2	Key	2	p-key, d-key, r-collar	20	F
3	Key	2	ret-collar, d-collar, r-key	15	S
4	Brush	0	r-collar	20	F
5	Brush	2	ret-collar, r-brush	30	S
6	Collar	2	r-collar	10	S
7	Key	4	r-collar	10	F
8	Brush	2	n-package, r-brush	15	S
9	Key	2	r-key	20	S
10	Package	4	n-brush, r-key	20	F
11	Brush	4	p-key	17	F
12	Brush	0	ret-key, r-brush	18	S
			November 8, 8:45 a.m. (glove, package, brush)		
1	Glove	2	r-glove promptly	10	S
2	Package	3	p-glove, looks out window, turns and d-glove, r-package	16	?
3	Brush	4	goes to window and looks out, turns, r-brush	15	S
4	Package	2	p-glove, d-glove, r-package	15	?
5	Brush	2	approaches slowly and r-package	15	F
6	Glove	2	p-glove, d-glove, r-package	25	F
7	Brush	4	p-glove, goes to window, returns to objects, r-glove and brush (window appeared to be distracting dog, so shade was drawn)	35	?
8	Glove	2	p-glove, d-glove, r-package	20	F
9	Glove	2	ret-with package, p-glove, r-package and glove	30	?
10	Brush	0	r-brush promptly	10	S
11	Package	5	r-package promptly	20	S
12	Brush	2	r-brush promptly	15	S
			November 10, 10:30 p.m. (package, brush, glove)		
1	Glove	3	moves slowly, r-glove	30	S
2	Brush	1	n-objects in order, r-glove	10	F
3	Glove	1	r-brush	15	F
4	Package	1	r-brush	15	F
5	Glove	1	r-glove	5	S
6	Brush	0	p-package, walks toward window, r-package	20	F
7	Brush	1	p-glove, d-glove, r-brush	20	?
8	Package	0	r-package	10	S
9	Brush	2	r-package	10	F
10	Brush	1	ret-package, d-package, r-brush	30	S
11	Glove	1	r-package	15	F
12	Glove	0	ret-package, appears tired, looks out window	30	F

Total number of responses.......... 36
Failures.......... 15
Successes (certain).......... 16
Successes (doubtful).......... 5

* n = noses; p = picks up; d = drops; r = retrieves; ret = returns.

although not when it was placed up on edge. The brush was also avoided when the stiff fibres were upturned and likely to irritate his nose, but was picked up readily enough when turned the opposite way. Strict control of this factor was not possible at the time, otherwise we feel the results of the test would have been more satisfactory.

The results here presented need to be greatly supplemented and the testing of Fellow extended in several directions before a true evaluation of the dog's ability can be arrived at. However, there would seem to be no doubt that scores of associations between verbal stimuli and definite responses have been well fixated by the patient teaching of Mr. Herbert during the past several years. The evidence for associations between verbal stimuli and objects or places would doubtless be forthcoming if a test were arranged in which object-discrimination could be made without the element of delay between stimulus and response entering in. We hesitate to make an interpretation of the present findings in terms of the dog's capacity for making a delayed reaction, on account of the meagreness and inconclusiveness of the data. In the type II command, which really includes the retrieving-objects test, we have a delayed reaction in which the essential signal for response is an auditory associate of the object, or locality in space, in connection with which the response must occur. Since the auditory stimulus gives no clue as to the localization of the object or place, orientation cannot be had as in the usual delayed reaction situation by the maintenance of gross bodily attitudes. If further tests should reveal certain evidence of such ability, as is more than suggested by the results here reported, then the dog would merit a much higher rank in the scale of mental evolution than most of us have been willing to accord him in the past.

This paper was read by the senior author before the Galton Society, Museum of Natural History, New York City, in connection with a demonstration of Fellow by Mr. Herbert before the Society on Friday, December 2, 1927.

LIST OF LITERATURE

(1) Anrep, G. V. 1920. Pitch discrimination in the dog. J. Physiol., 53, 367–385.

(2) Binet, Alfred and Passy, J. 1896. Congres de l'associat. pour l'avanc. des Scienc. Bordeaux.

(3) Bingham, H. C. 1916. Setting reactions of bird dogs to turtles. J. Animal Behav., 6, 371–373.

(4) Buytendijk, F. J. J. 1921. L'odorat du chien. Arch. néerl. Physiol., 5, 434–457.

(5) Buytendijk, F. J. J. and Hage, J. 1923. Sur la valeur de réaction de quelques excitants sensoriels simples dans la formation d'une habitude par les chiens. Arch. néerl. Physiol., 8, 215–233.

(6) Colvin, S. S. and Burford, C. C. 1909. The color perception of three dogs, a cat and a squirrel. Psychol. Monog., 11, No. 44, 48 p.

(7) Craig, W. 1924. The dog as a detective. Scient. Mo., 18, 38–47.

(8) Diederich, H. W. and Johnson, H. A. 1909. Police and work dogs in Europe. U. S. Dept. Commerce and Labor. Bureau of Manufactures. 1–16.

(9) Edinger, L. 1914. Zur Methodik in der Tierpsychologie. 1. Der Hund. Zsch. Psychol., 70, 101–124.

(10) Gates, Elmer. 1895. The science of mentation. Monist, 5, 574–597.

(11) Gilman, Elisabeth. 1921. A dog's diary. J. Comp. Psychol., 1, 309–315.

(12) Graber, Vitus. 1884. Grundlinien zur Erforschung des Helligkeits-und Farbensinnes der Thiere. Prag, 1884.

(13) Hamilton, G. V. 1907. An experimental study of an unusual type of reaction in a dog. J. Comp. Neur. and Psychol., 17, 329–341.

(14) ———. 1911. A study of trial and error reactions in mammals. J. Animal Behav., 1, 33–66.

(15) Heitzenroeder, C. 1913. Ueber das Verhalten des Hundes gegen einige Riechstoffe. Zsch. Biol., 62, 491–507.

(16) Henning, Hans. 1919. Geruchsversuche am Hund. Zsch. Biol., 70, 1–8.
(17) Himstedt, F. and Nagel, W. A. 1902. Versuche über die Reizwirkung verschiedener Strahlenarten auf Menschen- und Tieraugen. Festschrift der Albrecht-Ludwigs-Universität in Freiburg, p. 259.
(18) Hunter, W. S. 1913. The delayed reaction in animals and children. Behav. Monog., 2, No. 6, 86 p.
(19) Johnson, H. M. 1912. The talking dog. Science, 35, 749–751.
(20) ———. 1913. Audition and habit formation in the dog. Behav. Monog., 2, No. 8, 78 p.
(21) ———. 1914. A note on the supposed olfactory hunting-responses of the dog. J. Animal Behav., 4, 76–78.
(22) ———. 1914. Visual pattern discrimination in the vertebrates. II. Comparative visual acuity in the dog, the monkey and the chick. J. Animal Behav., 4, 340–361.
(23) ———. 1916. Visual pattern discrimination in the vertebrates. V. A demonstration of the dog's deficiency in detail-vision. J. Animal Behav., 6, 205–221.
(24) Jong, H. D. 1918. Recherches sur la formation d'idées chez le chien. Arch. néerl. Physiol., 3, 491–527.
(25) Kalischer, Otto. 1907. Zur Function des Schläfenlappens des Grosshirns. Eine neue Hörprüfungsmethode bei Hunden; zugleich ein Beitrag zur Dressur als physiologischer Untersuchungsmethode. Sitzber. Akad. Wiss., Berlin, Jahrgang 1907, 204–216.
(26) ———. 1909. Weitere Mitteilung ueber die Ergebnisse der Dressur als physiologischer Untersuchungsmethode auf den Gebieten des Gehör-, Geruchs- und Farbensinnes. Arch. Anat. Physiol., physiol. Abt., 1909, 303–322.
(27) Larguier des Bancels, J., and Claparède, E. 1913. A propos du chien de Mannheim. Arch. psychol., 13, 377–379.
(28) Löhner, L. 1926. Untersuchungen über die Geruchsphysiologische Leistungsfähigkeit von Polizeihunden. Arch. ges. Physiol., 212, 84–94.
(29) Lubbock J. (Avebury). 1888. On the senses, instincts and intelligence of animals with special reference to insects. New York, Appleton, 292 p.
(30) Mackenzie, W. 1913. Le problème du chien pensant de Mannheim. Arch. psychol., 13, 312–376.
(31) Meyer, E. M. 1895. Some experiments on the reaction-time of a dog. Studies from the Yale Psychol. Lab., 3, 96–97.
(32) Morgulis, Sergius. 1914. The auditory reactions of the dog studied by the Pawlow method. J. Animal Behav., 4, 142–145.
(33) Munk, Hermann. 1890. Ueber die Functionen von der Grosshirnrinde. Berlin, 320 p.
(34) Nicolai, G. F. 1907. Die Physiologische Methodik zur Erforschung der Tierpsyche, ihre Möglichkeit und ihre Anwendung. J. Psychol. Neur., 10, 1–27.
(35) Pavlov, I. P. 1927. Conditioned reflexes: an investigation of the physiological activity of the cerebral cortex. Oxford Univ. Press, 430 p.
(36) Romanes, G. J. 1887. Experiments on the sense of smell in dogs. Nature, 36, 273–274.
(37) Rothmann, Max. 1908. Ueber die Ergebnisse der Hörprüfung an dressierten Hunden. Arch. Physiol., 1908, p. 103.
(38) Samojloff, A. and Pheophilaktowa, A. 1907. Ueber die Farbenwahrnehmung beim Hunde. Zentbl. Physiol., 21, 133–139.
(39) Seffrin, L. 1915. Ueber die kleinsten noch wahrnehmbaren Geruchsmengen einiger Riechstoffe beim Hunde. Zsch. Biol., 65, 493–512.
(40) Schiche, O. E. 1922. Beobachtungen und Versuche an Junghunden der Gebrauchshundrassen. J. Psychol. Neur., 27, 227–231.
(41) Shepherd, W. T. 1915. Tests on adaptive intelligence in dogs and cats as compared with adaptive intelligence in Rhesus monkeys. Amer. J. Psychol., 26, 211–216.
(42) ———. 1919. On sound discrimination in dogs. Amer. J. Psychol., 30, 291–294.
(43) Slonaker, J. R. 1897. A comparative study of the area of acute vision in vertebrates. J. Morph., 13, 448–496.
(44) Smith, E. M. 1912. Some observations concerning color vision in dogs. Brit. J. Psychol., 5, 119–203.
(45) Stone, C. P. 1921. Notes on light discrimination in the dog. J. Comp. Psychol., 1, 413–431.
(46) Sutherland, A. H. 1917. Complex reactions of the dog: a preliminary study. Psychol. Monog., 23, No. 100, 241–265.
(47) Swift, W. B. Demonstration eines Hundes den beide Schlaefenlappen exstirpiert worden sind. Neur. Zentbl., 29, 686–688.
(48) ———. 1912. Physiological results in reactions to tone before and after extirpation of the temporal lobes. J. Animal Behav., 2, 225–228.

(49) Szymanski, J. S. 1913. Lernversuche bei Hunden und Katzen. Arch. ges. Physiol., 152, 307–338.

(50) ———. 1918. Abhandlungen zum Aufbau der Lehre von den Handlungen der Tiere. Arch. ges. Physiol., 170, 1–244.

(51) ———. 1918. Versuche über die Fähigkeit der Hunde zur Bildung von optischen Association. Arch. ges. Physiol., 171, 317–323.

(52) ———. 1920. Motorische und sensorielle Tiertypen. Biol. Zentbl., 40, 558–562.

(53) Thorndike, E. L. 1898. Animal intelligence. An experimental study of the associative process in animals. Psychol. Monog., 2, No. 8, 109 p.

(54) Walton, A. C. 1915. The influence of diverting stimuli during delayed reaction in dogs. J. Animal Behav., 5, 259–291.

(55) Watson, J. B. 1914. Behavior: An introduction to comparative psychology. New York, Henry Holt, 439 p.

(56) Williams, J. A. 1926. Experiments with form perception and learning in dogs. Comp. Psychol. Monog., 4, No. 18, 70 p.

(57) Yerkes, R. M. and Morgulis, Sergius. 1909. The method of Pawlow in animal psychology. Psychol. Bull., 6, 257–273.

(58) Yerkes, R. M. and Watson, J. B. 1911. Methods of studying color vision in animals. Behav. Monog., 1, No. 2, 90 p.

THE HISTORY OF WHALES—THEIR ADAPTATION TO LIFE IN THE WATER

By REMINGTON KELLOGG

Bureau of Biological Survey, United States Department of Agriculture

CETACEANS are air-breathing warm-blooded mammals, generally having pointed heads, torpedo-shaped bodies, fin-like fore limbs, and horizontal caudal flukes. All external structures and protruding organs which might offer resistance to the water have been either eliminated or sunk below the surface level. This group embraces the extinct zeuglodonts (Archaeoceti), the whalebone whales (Mysticeti), and the toothed whales (Odontoceti), including porpoises, dolphins, beaked whales, and sperm whales.

Naturalists and sea-faring people have been recording their observations on whales for many centuries and, although early literature dealing with the group contains much that is fanciful and little that is real, it is evident that whales and porpoises have long been objects of interest to mankind. The existing cetaceans are so well adapted for a continuous life in the water that naturalists of the Middle Ages believed that they must belong to the fish tribe. John Ray (1671) was one of the first to discover that the relationships of the cetaceans were with land mammals rather than with the fishes. Subsequently these animals attracted the interest of other naturalists, many of whom published their observations, so that the literature relating to cetaceans now comprises several thousand titles. Study of the anatomy of living whales and the bones of extinct species has led to many interesting speculations.

Why the progenitors of the whales forsook the land is a tempting field for speculation, but while we do know that some archaic land mammals were induced to take to water, the reasons for this action do not admit of direct proof. It is possible that the forebears of the whales may have thus found either a safe refuge from more active predatory types, or an abundance of food in shallow water and along the shores, and available data indicate that the late Sir William Flower (1883) was not far wrong when he suggested that the ancestors of whales frequented fresh water and that search for their remains should be made in the fresh water deposits of the Cretaceous period. Many anatomical and physiological adjustments were necessitated as these mammals became better adapted to their aquatic surroundings, and those which became perfectly adapted to this sort of habitat had to undergo a number of fundamental structural alterations to cope with the new conditions. Some of the modifications which were tried out in the course of geological time proved more successful than others, and as a result we find that old species continuously disappeared and new ones took their places. In consequence of the substitution of certain parts and the complete elimination of others, it is not surprising that living repre-

sentatives are often quite unlike the original stock from which they have descended.

Whales at one time, geologically speaking, were land mammals and, although highly modified in some respects, they still retain all the typical mammalian features. Like land mammals they suckle their young and retain vestiges of their former coating of hair. With the passage of time their fore limbs have been modified to function as pectoral flippers, and their tail has been provided with caudal flukes to function as an organ for propulsion. No traces of hind limbs have been found in any of the living toothed whales with the exception of the sperm whale (*Physeter catodon*), but nevertheless we are fairly certain that these were present in the progenitors of the Cetacea, since the whalebone whales have one or two vestigial limb bones buried deep in the flesh of the pelvic region. Much more profound changes have occurred in the "soft parts" and in the physiological adjustments of their organs to an aquatic life. The bodily organization of living whales shows us what has been accomplished in the way of adaption, but it affords no proof of how this has come about, and for evidence of this sort we must look to the record in the rocks. The skeleton is the framework upon which the muscles and organs are attached, and by studying these "hard parts" and endocranial casts one can infer some of the changes which were taking place in the so-called "soft parts." Porpoises are found in both fresh and salt water, while the whalebone whales are almost exclusively pelagic. Both of these two groups of living cetaceans have followed different paths of anatomical adjustment to fit themselves to this or that manner of living.

To show that adaptation to life in the water is a complex biological transition for a mammal formerly accustomed to land conditions and that such an adaptation has been clearly demonstrated by collateral investigations along the lines of palaeontology, anatomy, embryology, and physiology is the object of this résumé. From the very nature of the evidence it is not surprising that there should be some divergence of opinion as to the details of this biological process, but there is little or no conflict as regards the fundamental principles underlying the views that are based on ascertainable facts.

Some ten years ago the writer was invited to prepare a report on the fossil marine mammals as a part of a research program planned by Dr. John C. Merriam for a study of the extinct vertebrate faunas of the Pacific Coast and Great Basin Provinces of North America, and during the past six years this work has been supported by the Carnegie Institution of Washington. In the course of this investigation the writer has had the opportunity to study the collections of fossil and recent cetaceans in the United States National Museum, the American Museum of Natural History, the Museum of Comparative Zoology, the Museum of Palaeontology of the University of California, and the California Academy of Sciences. In the matter of illustrations the writer has had the able coöperation of Mr. Sydney Prentice, who has prepared practically all of the line drawings used in this essay. In cases where no complete skull has been available the illustration is based on two or more skulls which mutually supplement one another so far as missing parts are concerned, but in each instance the skulls selected for this purpose are conspecific and were obtained from the same geological horizon.

GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION

The difficulties that beset one who is engaged in a study of whales, past and present, are in no small measure due to the practically world wide distribution of these pelagic mammals during the Tertiary period and the consequent lack of adeqate material from many parts of their range. Not so many years ago the scope of our geographic knowledge of fossil whales was confined to Europe and North America, but it has been slowly extended until it now includes portions of Africa, South America, Seymour Island in the Antarctic, Australia, New Zealand, and Japan. No remains of fossil whales have as yet been described from continental Asia, nor from the numerous islands which dot the Atlantic, Pacific, and Indian oceans. The imperfection of the geological record is an accepted fact, but probably our knowledge of the past history of the whales would present fewer gaps had a concerted effort been made to assemble systematically collections of fossil pelagic mammals. Marine formations that are known to contain remains of fossil pelagic mammals occur on nearly all continental masses with the exception of Asia. If modern methods of collection and preservation of specimens were applied, many of these marine formations should yield material which would throw additional light on the evolution of this interesting group.

Search for remains of fossil whales has never been prosecuted with the same energy and zeal as for many other orders of vertebrates, and a large number of the forms now known are based on material obtained from thirty to one hundred years ago. Owners of quarries, brick works, marl pits, and diatomaceous deposits have contributed to interested scientists a large part of the fossil whales that have been mentioned in scientific periodicals during the past century. Purely fortuitous circumstances, however, have resulted in the acquisition of some rather large and important collections. When the fortifications of Antwerp were under construction, in the years 1861 to 1863, hundreds of whale skeletons were found in the excavations, and many of them are preserved in the Royal Museum of Natural History at Brussels. As early as 1868 interested officials and employees of the fertilizer companies exploiting the so-called Ashley phosphate deposits of South Carolina noted the extraordinary variety and profusion of fossil remains of vertebrated animals that were brought to light in the course of their operations. Specimens were preserved in company offices and in the homes of interested citizens. In time important collections were built up, and many of these found their way into institutions and museums, where they have been carefully preserved for their scientific value.

Geologically and geographically whales have had a long and widespread range. Some of the living cetaceans are great travellers and apparently wander from one shore to another in the course of their migrations, while others exhibit decided preferences for limited oceanic areas. The extent of the migrations of whales is largely a matter of conjecture, but the evidence points to the conclusion that some species travel from the South Pacific to the North Pacific and vice versa. Sei whales have been taken in Japanese waters with ectoparasites of South Pacific origin (Andrews, 1916). In the Atlantic ocean conditions are similar. Information from other sources indicates that whales pass from one ocean to another around Cape

TABLE 1

Geological and geographical distribution of whales

	EOCENE								OLIGOCENE				MIOCENE					PLIOCENE			QUATERNARY
	Lower				Middle		Upper		Lower	Middle	Upper		Lower	Middle		Upper		Lower	Middle	Upper	
	Montian	Thanetian	Sparnacian	Ypresian	Lutetian	Auversian	Bartonian	Ludian	Lattorfian	Rupelian	Casselian	Aquitanian	Langhian	Helvetian	Tortonian	Sarmatian	Pontian	Plaisancian	Astian	Sicilian	
ARCHAEOCETI																					
Protocetidae:																					
Eocetus						A															
Pappocetus			?A																		
Protocetus					A																
Prozeuglodon						A	A														
Dorudontidae:																					
Dorudon								N													
Kekenodon											Z										
Phococetus												E									
Zygorhiza							N														
Basilosauridae:																					
Basilosaurus						A	E A–N	E													
ODONTOCETI																					
Agorophiidae:																					
Agorophius								N													
Xenorophus								N													
Squalodontidae:																					
Colophonodon																N					
Metasqualodon													Au								
Microcetus											E										
Microsqualodon													E								
Microzeuglodon													E								
Neosqualodon													E								
Parasqualodon													Au								
Phoberodon													S								
Prionodelphis																		S			
Prosqualodon													S–Z								
Rhytisodon													E								
Saurocetus																N					
Squalodon													E	E–N	N	E–N					
Trirhizodon													E	E							
Iniidae:																					
Anisodelphis																		S			
Hesperocetus																	N				
Ischyrorhynchus																		S			
Pontoplanodes [= *Saurodelphis*]																		S			
Proinia													S								
Ziphiidae:																					
Anoplonassa																N					

Abbreviations: A., Africa; Au., Australia; E., Europe, including Russia; J., Japan; N., North America; S. South America; Z., New Zealand; ?, indicates some uncertainty as to the age or identity; [?], indicates some uncertainty as to family position.

TABLE 1—*Continued*

	EOCENE								OLIGOCENE				MIOCENE					PLIOCENE			
	Lower				Middle		Upper		Lower	Middle	Upper		Lower	Middle		Upper		Lower	Middle	Upper	
	Montian	Thanetian	Sparnacian	Ypresian	Lutetian	Auversian	Bartonian	Ludian	Lattorfian	Rupelian	Casselian	Aquitanian	Langhian	Helvetian	Tortonian	Sarmatian	Pontian	Plaisancian	Astian	Sicilian	QUATERNARY
Ziphiidae—*Cont:*																					
Belemnoziphius																N					
Berardiopsis																			E		
Cetorhynchus														E		E					
Choneziphius																E–N			E		
Diochotichus													S								
Eboroziphius																N					
Mesoplodon																E–N			E		
Mioziphius																E					
Palaeoziphius																E					
[?] *Pelycorhamphus*																N					
Proroziphius																N					
Squalodelphis													E								
Ziphioides															E						
Delphinidae:																					
Acrodelphis													E		N	E					
Agabelus															N						
Argyrocetus													S								
Belosphys															N						
Ceterhinops																N					
Champsodelphis														E	E	E					
Cyrtodelphis [= *Schizodelphis*]													E–A	E	E–N	E–N	E				
Delphinodon															N						
Delphinopsis																E					
Delphinavus													N								
Delphinus																		E	E		
Eoplatanista													E								
Eurhinodelphis															N	E–J					
Globicephala																					N
Heterodelphis															E	E					
Ixacanthus															N						
Iniopsis													E								
Kentriodon															N						
Lophocetus															N						
Macrochirifer																E					
Orcinus																			E		
Palaeophocaena																E					
Phocaenopsis																					Z
Phocaena															E?						
Pithanodelphis																E					
Pomatodelphis														E		N					
Priscodelphinus															N						
Protodelphinus													E								

TABLE 1—*Continued*

	EOCENE								OLIGOCENE				MIOCENE					PLIOCENE			QUATERNARY
	Lower				Middle		Upper		Lower	Middle	Upper		Lower	Middle		Upper		Lower	Middle	Upper	
	Montian	Thanetian	Sparnacian	Ypresian	Lutetian	Auversian	Bartonian	Ludian	Lattorfian	Rupelian	Casselian	Aquitanian	Langhian	Helvetian	Tortonian	Sarmatian	Pontian	Plaisancian	Astian	Sicilian	
Delphinidae—*Cont:*																					
Protophocaena																E					
Pseudorca																				E–J	
Rhabdosteus															N						
Steno																		E	E		
Stereodelphis														E							
Tretosphys															N						
Tursiops														E?				E	E	E	
Ziphiodelphis													E								
Delphinapterus																					N
Monodon																				E	N
Lonchodelphis																			N		
Pontistes																		S			
Pontivaga																		S			
Stenodelphis																					N
Platanistidae:																					
Zarhachis															N						
Kogiidae:																					
Kogia																				J	
Physeteridae:																					
Aulophyseter														N							
Balaenodon																			E		
Diaphorocetus													S								
Dinoziphius																N					
[?] *Graphiodon*																N					
Hoplocetus														E							
Idiophyseter															N						
Idiorophus													S								
Ontocetus														J	N	N					
Orycterocetus															N						
Physeter																N		E	E		N
Physeterula																E					
Physetodon																		Au			
Placoziphius																E					
Priscophyseter																			E		
Prophyseter																E					
Scaldicetus													?E			E		?Au			
Scaptodon													Au								
Thalassocetus																E					
Incertae sedis:																					
Agriocetus												E									
Archaeodelphis								N													
Patriocetus												E									

TABLE 1—*Concluded*

	EOCENE								OLIGOCENE				MIOCENE					PLIOCENE			QUATERNARY
	Lower				Middle		Upper		Lower	Middle	Upper		Lower	Middle		Upper		Lower	Middle	Upper	
	Montian	Thanetian	Sparnacian	Ypresian	Lutetian	Auversian	Bartonian	Ludian	Lattorfian	Rupelian	Casselian	Aquitanian	Langhian	Helvetian	Tortonian	Sarmatian	Pontian	Plaisancian	Astian	Sicilian	
MYSTICETI																					
Cetotheriidae:																					
Amphicetus																		E			
Cephalotropis															N						
Cetotheriomorphus																E					
Cetotheriopsis												E	S								
Cetotherium													?N			E					
Eucetotherium																E					
Heterocetus																		E			
Herpetocetus																E					
Plesiocetus Auct.													S		E	E					
Isocetus																E					
Mesocetus														E		E					
Metopocetus															N						
Pachyacanthus																E					
Pachycetus										E											
Parietobalaena															N						
Plesiocetopsis															N	N		E			
Rhegnopsis															N						
Siphonocetus															N						
Tretulias															N						
Ulias															N						
Balaenopteridae:																					
Balaenoptera																	N	E	E		N
Burtinopsis																			E		
Cetotheriophanes																		E			
Idiocetus																				E	
Megaptera																	N		E		N
Megapteropsis																		E			
Mesoteras																N					
Plesiocetus V.B.																		E			
Balaenidae:																					
Balaena																		E	E	E	
Balaenotus																			E		
Balaenula																			E		
Eubalaena																					S
Morenocetus													S								
Notiocetus																		S			
Palaeocetus																			E		
Protobalaena																		E			

Horn and Cape of Good Hope. The possibilities for the dispersal of cetaceans are exceptionally great, in view of the absence of physical barriers, and apparently the chief controlling factor is the food supply. Of the thirty genera of living toothed whales, four are restricted to rivers, occurring not only in their estuaries, but occasionally in their tributaries as well. One or two genera, like *Sotalia* and *Steno*, are essentially tropical in their distribution and are represented by one or more species in the Atlantic, Pacific, and Indian Oceans. Many odontocete genera are more widely distributed, and some of them, especially the killer (*Orcinus*), the lesser killer (*Pseudorca*), the common dolphin (*Delphinus*), the sperm whale (*Physeter*), and one of the beaked whales (*Ziphius*) are practically cosmopolitan. The bowhead (*Balaena mysticetus*), which frequents the Arctic seas, and the pigmy whale (*Neobalaena marginata*) of New Zealand waters appear to be restricted in their dispersal by climatic conditions. Some of the whalebone whales are without doubt the largest mammals that have ever lived. No mammal, not even the zeuglodonts, has attained the proportions of the blue or sulphur bottom whale (*Sibbaldus*), individuals of which have measured 98 feet in length. Not all of the living whalebone whales are so large, and one of the smallest is the pigmy whale (*Neobalaena*), which rarely reaches a length of more than 20 feet.

The geological and geographical distribution of whales assembled in table 1 shows many gaps, and the discontinuous distribution in many instances is due either to the inadequacy of the material collected or to lack of effort in areas where material could be secured.

ARCHAEOCETI

The oldest known relatives of the typical cetaceans are found in some of the oldest Tertiary rocks; that is in those that correspond in age to the early part of the Age of Mammals. Even these archaic mammals were well specialized in many respects for a pelagic life. It so happened that the first notice of these mammals was based on a few fragments found in the Eocene of southeastern Caldwell Parish, Louisiana, near the Ouachita River. Dr. Harlan (1834) believed that they belonged to a giant reptile, to which he gave the name *Basilosaurus*, but Owen (1839) was able to demonstrate that they were a part of some colossal mammal, for which he proposed to substitute the name *Zeuglodon*, in allusion to the yoke-like appearance of the cheek teeth. So far as known the oldest zeuglodonts had already acquired a complicated organ for hearing, they retained a well developed olfactory apparatus, but their brain structure as shown by casts indicates that their sight was defective. Although they tried out braincases of somewhat different proportions, the main path of their evolutionary advance seems to have been limited to a remodeling of the cheek teeth. Complete skeletons of the early Eocene zeuglodonts have never been found, but those of the Upper Eocene had lost the functional use of their hind limbs, for the femur was vestigial and the pelvic girdle atrophied.

It is neither desirable nor possible to recount in detail here the various views that have been advanced regarding the affinities of the zeuglodonts. In recent years the concept that they are related to if not descended from the primitive insectivore-carnivore stock has had wide acceptance. Morphologically they seem relatively near to the typical whales and porpoises, although it is not necessary to assume that any known zeuglodont is ancestral to some particular kind of whale, for the zeuglodont skull in its general structure appears to be divergent from

rather than antecedent to the line of development that led to the telescoped condition of the braincase seen in skulls of typical cetaceans. On the contrary it is more probable that they are collateral derivatives of the same stock from which the true Cetacea sprang. No tendency toward cranial telescoping has been observed in any of the zeuglodonts, yet they possess certain structural features which are morphologically intermediate between early land mammals and true cetaceans. Miller (1923) holds that the known zeuglodonts are not directly ancestral to any of the recent whales, and contends that the transition from this type of skull to the toothed whale (Odontoceti) skull involves simpler principles than is the case for the whalebone (Mysticeti) whales. Curiously enough, periotic bones of both the whalebone and the toothed whale types have been found attached to skulls of zeuglodonts.

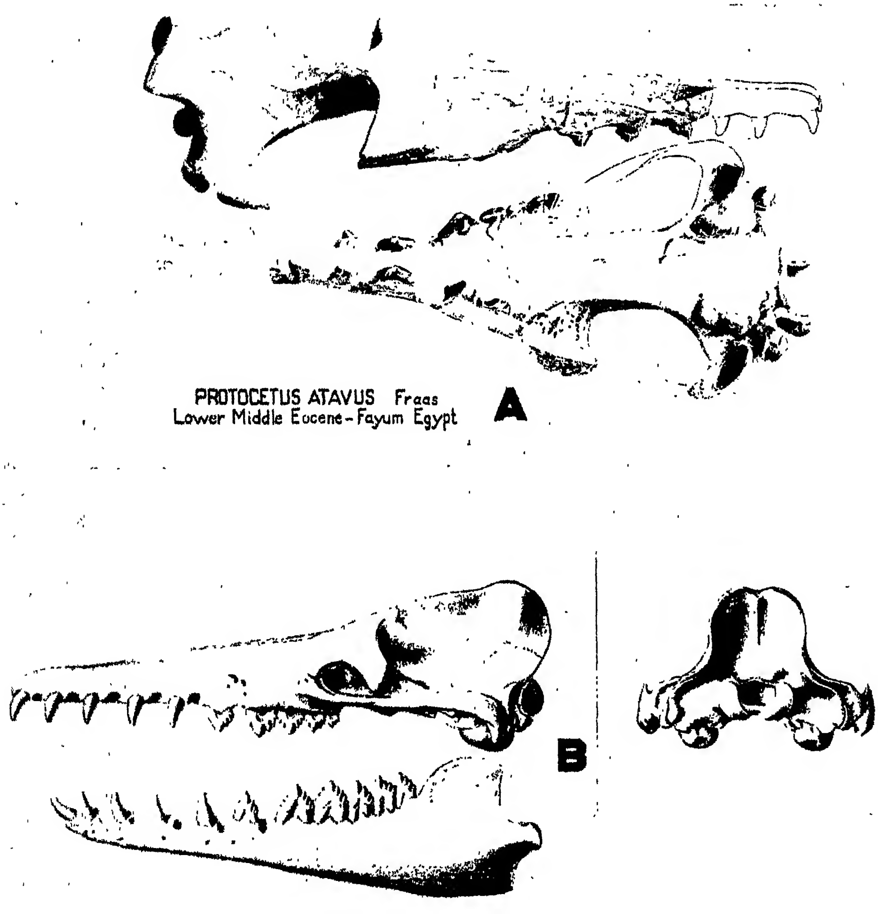


Fig. 1. Skulls of Zeuglodonts

A. Dorsal and ventral views of skull of *Protocetus atavus* (after Fraas). *B*. Lateral and posterior views of skull of *Prozeuglodon stromeri* (after Stromer).

The bones in the rostrum and cranium of

these zeuglodonts retain their normal mammalian relationships; the facial region is elongated without overlapping of the bones. The braincase is narrow and elongate, and not shortened antero-posteriorly as in living whales, for all have a remarkable elongated intertemporal constriction and large temporal fossae. The parietals are normal in their relation to other bones and meet on the mid-line to form a sagittal crest. The exoccipitals are already extended laterally, and a lambdoid crest is developed. The articular surface on the zygomatic process for the lower jaw tends to assume the peculiar vertical position of true Cetacea. All known zeuglodont skulls have a flattened forehead and a broadened supraorbital process of the frontal, extended laterally beyond the jugal portion of the zygomatic arch, and arched at the extremity. The nasal bones are elongated and do not encroach upon the frontals, but lie almost wholly in front of the level of the anterior margins of the supraorbital processes. The posterior portion of the nasal cavity is relatively undisturbed, and turbinal bones are present. The opening leading to the nostrils has been moved backward to the level of the first upper premolar, about halfway to the orbit. The proximal end of the maxillary abuts against the supraorbital process of the frontal superiorly and inferiorly projects backward below the latter to accommodate the posterior molars. The premaxillary has an ascending process which does not reach the frontal, but terminates behind the antorbital foramen (above Pm^2 or Pm^3) and anteriorly is conspicuously extended beyond the extremity of the maxillary. Apparently the mouth was used mainly as a pair of forceps, with long, narrow, beak-shaped rostrum, in which the anterior teeth are widely spaced. The incisive foramina were eliminated by the linear contact of the premaxillaries along the mid-line. The palatines do not extend forward beyond the level of the posterior premolar, but the bony palate is prolonged backward by outgrowths of the palatines and pterygoids. The tympanic bulla has already acquired an involucrum. If our interpretation of the zeuglodont skull is correct, a somewhat greater use was made of that part of the tooth row which serves for grasping food than of that which serves for grinding, or shearing, and consequently the incisors and anterior cheek teeth increased in size. The premolars became heavier, with higher crown points, but the molars were weakened, and the second upper molar lost its predominance. The cheek teeth of later zeuglodonts have several accessory cusps on their anterior and posterior cutting edges. The earlier zeuglodonts have premolars and molars with vestiges of the inner portion of the crown and a reduced postero-internal cusp. The later zeuglodonts have lost the last upper molar, and the remnant of the postero-internal cusp disappeared with the third root.

So far as known to the writer, no fossil Archaeoceti have been found in the Lower Eocene, though it is not unlikely that a zeuglodont, *Pappocetus lugardi*, recently described by Andrews (1920) will eventually prove referable to that period. This small species was found in the Ombialla District of Southern Nigeria in hard pyritous clay and is represented by portions of two left mandibles belonging to immature individuals, for the last molars are not cut in either specimen. The mandibles of this zeuglodont apparently possessed the full eutherian dentition, with 3 incisors, 1 canine, 4 premolars, and 3 molars in each lower jaw, and it is especially interesting on account of the carnivore-like characters of the cheek teeth. The premolar-molar series, with the exception of the first lower

premolar, possess a well defined cingulum and retain distinct vestiges of the inner portion of the crown. The premolars have a crown with one large cusp and a rudimentary basal posterior cusp. The fourth lower premolar has the longest antero-posterior diameter. Each of the three molars has a large anterior cusp and a smaller posterior cusp. In contrast to zeuglodonts of later stages the second incisor is relatively large.

In passing from the lower Middle Eocene to the uppermost Eocene, zeuglodonts are encountered which reveal some of the progressive stages in the remodelling of the cheek teeth as well as the reshaping of the occipital region of the skull and other skeletal changes.

Several faunas of these zeuglodonts have been discovered in the Middle and Upper Eocene deposits of the Fayum in Egypt. These rocks are older than our own Gulf Coastal Plain deposits and have yielded several rather distinct types of zeuglodonts. The oldest geologically is a somewhat generalized form, *Protocetus atavus*, described by Fraas in 1904, from the basal member of the Lower Mokattam stage near Cairo. The skull of this small species is less than two feet in length and bears little resemblance to living cetaceans. The normal eutherian dentition is present. In common with the oldest land mammals, there is a marked difference between the anterior grasping teeth and the posterior cutting teeth. In contrast to zeuglodonts of later stages of the Eocene, the teeth of *Protocetus* do not bear step-like cusps on their anterior and posterior cutting edges, and distinct vestiges of the inner portion of the crown are retained. The two posterior upper premolars and the three molars have three roots and a remnant of the postero-internal cusp. Both Fraas and Andrews have pointed out that *Protocetus* is a highly important link in the history of the Archaeoceti, for here we have a skull that is typically zeuglodont in general form combined with a dentition that is essentially that of a creodont. In some characters, such as the peg-like odontoid and the relatively long centrum, the axis of the lower Middle Eocene *Protocetus* approaches the type of cervical found in the carnivores. The late Dr. C. W. Andrews of the British Museum of Natural History contended that the zeuglodonts probably originated on the northern shores of Africa in the early part of the Tertiary period and that *Protocetus* was an annectant form between the later zeuglodonts and the earlier creodonts.

In the upper Middle Eocene a slightly more advanced type of zeuglodont, *Prozeuglodon atrox* (Andrews, 1906) makes its appearance. It should be noted here that Professor Stromer (1908) has suggested that this may be a young individual of *Zeuglodon isis*. The skull of this species measures about 26 inches in length, and the occipital shield has the appearance of being less constricted above the condyles. The number of molars is uncertain, but otherwise it has the normal eutherian dentition. The cutting edges of the crowns of the molars and the three posterior premolars are serrated. $Pm.^3$, $Pm.^4$, and $M.^1$ have an enamel covered buttress, evidently the remnant of the postero-internal cusp, and in the premolars at least this buttress is supported by a distinct third root. *Prozeuglodon* has an axis with a short, blunt, rounded odontoid, while that of "*Zeuglodon*" is flattened above. Zeuglodonts of the Upper Eocene have an axis with a high massive neural spine, but the centrum and transverse processes are shortened. The evidence appears to be fairly clear that a shortening of the neck was brought about by a reduction of the centra of the cervical

vertebrae. A similar history is known for living cetaceans. *Prozeuglodon stromeri* is the representative of this series in the Upper Eocene. A fairly complete skeleton (Stromer, 1908), measuring about ten feet in length including the skull, which measures 28 inches, gives us a fairly adequate conception of this species.

Several diverse types of zeuglodont skulls, which appear to belong to four distinct series, have been found in the Upper Eocene. "*Zeuglodon*" *osiris* (Stromer, 1903) is probably the best known of the small zeuglodonts that make their appearance subsequent to the lower Middle Eocene. The skull of this species did not exceed 30 inches in length. The braincase is narrow, elongated, and high posteriorly, and the bones in the cranium retain their normal mammalian relationships. The skull of "*Zeuglodon*" *osiris* is remarkable for the narrowness of its occipital shield, the lateral portions of the lambdoid crest being sharply deflected backward so that this surface has the appearance of being constricted above the condyles. These modifications afford an increase in surface for attachment of jaw muscles and no doubt are correlated with increasing size and strength of the mandible. As compared with "*Zeuglodon*" *intermedius* the condyles and foramen magnum are smaller, the rostrum seems to be narrower, and perhaps the opening leading to the nostrils was situated farther back. In this series there is a tendency toward a narrowing of the occipital shield accompanied by a folding back of the lambdoid crests, resulting in increasing concavity of the surface above the foramen magnum. The sagittal crest increases in height, and the condyles and foramen magnum diminish in size. The cheek teeth of these two zeuglodonts are serrated on their anterior and posterior cutting edges, and the last upper molar is lost. According to Andrews (1923) the buttress or postero-internal cusp is reduced in size and apparently was not supported by a third root.

The depression of the occipital shield in the *Zygorhiza minor* series was accompanied by decreasing convexity of the lateral cranial walls and a rather pronounced folding backward of the lambdoid crest. This crest is exceptionally high and flaring, and is raised from 30 to 40 mm. above the lateral walls of the braincase. The rostrum has increased in length and slenderness, and the opening leading to the nostrils has moved farther backward, the interval between it and the orbit being about one-third the length of the rostrum. In *Zygorhiza minor* (Müller, 1849, and True, 1908), however, both ends of the premolar-molar series appear to have been reduced, inasmuch as the first upper single-rooted premolar and the third upper molar are missing on the cast of the type skull obtained from the Tyler museum. The first tooth of the upper premolar series of "*Zeuglodon*" *zitteli* according to Stromer (1903, p. 82) is likewise two-rooted. In the smaller zeuglodonts, such as *Zygorhiza minor* and *Prozeuglodon stromeri* (Stromer, 1908, No. Mn. 9, p. 110, pl. 4), the skull equalled approximately one-fifth of the total length of the skeleton, but in the colossal types like *Basilosaurus cetoides* not more than one-tenth of the total length.

The carnivorous zeuglodonts typified by *Basilosaurus cetoides* (Gidley, 1913) of the Gulf Coastal Plain of the United States, which attained a length of from 50 to 70 feet and whose skull measured approximately 5 feet in length, reached the flood tide of their evolutionary advance during late Eocene times. It seems to be generally conceded that gigantism is one of the indications of approaching extinction, but there must have been other contributing factors, for the Oligocene

zeuglodonts were much smaller and represent another line of descent. In later Eocene zeuglodonts the dentition is reduced by the loss of the third upper molar. The elimination of the postero-internal cusp of the cheek teeth was followed or accompanied by the loss of the third root. In the case of *Basilosaurus cetoides* of North America as well as "*Zeuglodon*" *isis* (Stromer, 1908) of the Fayum the cheek teeth have not more than two roots, and not even a vestige of the postero-internal cusp remains. The cheek teeth have a laterally compressed crown, that of the premolars serrated on both edges and that of the molars on one or both edges. The shoulder blade is cetacean-like, but the humerus has held more closely to the original form, retaining a well developed deltoid ridge, greater and lesser tuberosities, and a hinge-shaped distal articular surface. The sternum is relatively large and is made up of several sections. At least two of the small zeuglodonts, *Zygorhiza minor* and *Prozeuglodon stromeri*, have lumbar vertebrae with short centra and long articulating zygapophyses, while the large *Basilosaurus cetoides* and "*Zeuglodon*" *isis* have lumbars with greatly elongated centra, although the neural arches have remained short. This specialization is unique among mammals, for the greater part of the vertebral column is articulated only by the centra, the zygapophyses being separated by too wide an interval to function in the normal manner.

The short bodied zeuglodonts, such as *Zygorhiza minor*, which have a short neck, thoracic and lumbar vertebrae with high, broad neural spines, well developed transverse processes, and articulating zygapophyses, must have had a propelling mechanism of considerable strength, for among living cetaceans the most powerful swimmers have a vertebral column of this type. The conclusion can be drawn that these short bodied zeuglodonts propelled themselves by upward and downward strokes of the flukes, after the manner of living whales. They were therefore undoubtedly powerful swimmers, capable of diving or turning at will, and were equipped with a dentition admirably fitted for seizing and holding their prey.

Conversely the gigantic zeuglodonts, such as *Basilosaurus cetoides*, which have an elongated trunk and tail, the neck conspicuously shortened, thoracic and lumbar vertebrae with low neural spines and short transverse processes disproportionate to the length of the skeleton, and zygapophyses of all the trunk vertebrae with the exception of the first four or five dorsals, separated by increasing intervals proportional to length of centrum, could hardly have had a powerful propelling tail operating in the same fashion. On the contrary these details indicate that the tail was adapted for lashing, and that in swimming the animal progressed by marked sinuous or serpentine movements.

By the close of the Eocene period zeuglodonts had spread widely, for their remains have been found in Russia, England, and other localities in Europe, the Atlantic and Gulf Coastal plains of the United States, New Zealand, and Seymour Island in the Antarctic. A few of the smaller forms held over until near the close of the Oligocene.

TYPICAL CETACEA

The conclusion that cetaceans living and extinct have arisen from a multiserial stock appears to be borne out not only by osteological, but also by anatomical evidence. That at least three distinct lines of descent are represented among the known Cetacea is evidenced by the general acceptance among mammalogists of the three suborders, of which the Archaeoceti or zeuglodonts at present are known to

have been in existence at a more remote time than the Odontoceti or toothed whales; while the known geological history of the Mysticeti or whalebone whales is much shorter and does not date at present farther back than the Oligocene. The exigencies of an aquatic mode of living are such that the members of the several families of these three suborders assumed a similar outward appearance in conformity with streamline requirements such as have been forced upon many other unrelated groups of aquatic vertebrates, but there is no palaeontological evidence to support any assumption of a remodeling of originally unlike parts to a similar adaptive use. The directions in which the members of these three suborders, collectively and individually, subsequently developed were predetermined by peculiarities of structure in existence at or before the entrance upon a pelagic habitat. The resemblances between these three suborders are such as to suggest a rather close relationship of the original ancestral forms and common descent from some broad headed ancestral stock in which the critical cranial elements were united by squamous instead of dentate sutures. No extinct cetacean skull known holds proof of descent of an archaic toothed whale from any known zeuglodont, or presents structural conditions necessary to form the basis for the elaboration of the mysticete and odontocete types of skull from any common cetacean stock.

A mammalian skull is composed of a number of distinct bones, some of which build up a closed box to protect the nervous system; on the lower posterior bones of the skull are located the articular surfaces for the supporting atlas vertebra of the neck and the bones of the tongue, while others make up the jaws and the muzzle portions. The exposed surfaces of the several bones give origin to or afford insertion for the various muscles which are found in the region of the head. In the generalized type of skull, such as may be found in some of the early Tertiary land mammals, the individual bones exhibit certain mutual contact relationships, and this original architectural plan has been retained with few exceptions during the Cenozoic era by most orders of mammals. Changes in the relative size and shape of the individual bones occur frequently in the geological history of most groups, but there has been very little rearrangement of the bones themselves. Skulls of cetaceans other than zeuglodonts differ from those of all land mammals in that they exhibit an extreme type of remodeling and present alterations which have affected not only the relative size and shape of many of the individual bones, but also their mutual relations. Except for the zeuglodonts, the skulls of all known cetaceans show in some degree the effects of telescoping—that is, the braincase or the portion of the skull behind the rostrum has been shortened, mainly by the slipping of one bone over another or by interdigitation. Gerrit S. Miller (1923) has discussed the telescoping of the cetacean skull in considerable detail and has shown that this process proceeded according to two different plans, one of which is found in the whalebone whales (Mysticeti) and the other in the toothed whales (Odontoceti).

The departure from the generalized type of land mammal skull is most striking in living cetaceans, but even in the earliest known extinct genera of true whales (*Agorophius*, *Xenorophus*, and *Archaeodelphis*) the telescoping was well advanced. If the zeuglodonts and the archaic toothed whales did arise from terrestrial mammals during the Lower Eocene stage, then the rapidity with which they became so completely adapted for an aquatic life far

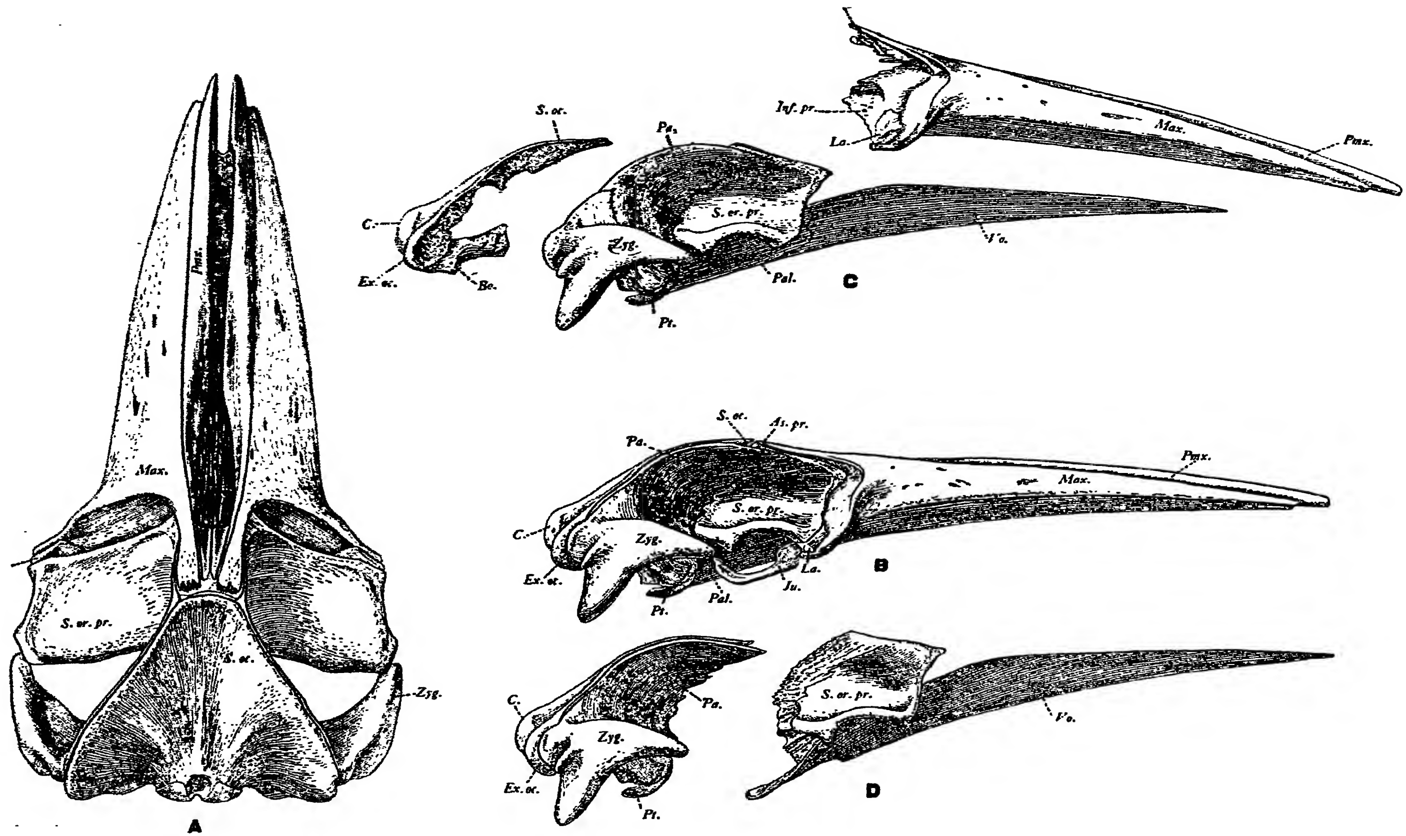


Fig. 2. Skull of Balaenoptera borealis, Young Male, Walnut Point, Virginia

A. Dorsal view. *B*. Lateral view. *C*. Lateral view of disarticulated skull, with rostrum and occipital shield detached. *D*. Lateral view of disarticulated skull, with frontal and vomer detached from braincase; the rostrum has been removed. The following abbreviations are used on the text figures: *Al.*, alisphenoid; *Al. gr.*, alveolar groove; *Ant. n.*, antorbital notch; *Ap. max.*, apophysis of maxillary; *As. pr.*, ascending process of maxillary; *Bo.*, basioccipital; *C.*, condyle; *Ect.*, ectethmoid; *Ex. oc.*, exoccipital; *f. inf.*, infraorbital foramen; *f. max.*, maxillary foramen; *f. olf.*, olfactory foramen; *f. pmx.*, premaxillary foramen; *Fr.*, frontal; *Inf. pr.*, infraorbital process of the maxillary; *Ju.*, jugal; *La.*, lachrymal; *Max.*, maxillary; *Max. cr.*, crest of maxillary; *Max. inc.*, maxillary incisure; *Max. t.*, maxillary tuberosity; *Mes.*, mesethmoid; *Mrc.*, ossified mesorostral cartilage; *Na.*, nasal; *Pa.*, parietal; *Pal.*, palatine; *Pmx.*, premaxillary; *p. max. f.*, posterior maxillary foramue; *Prs.*, presphenoid; *Pt.*, pterygoid; *S. oc.*, supraoccipital; *S. or. pr.*, supraorbital process of frontal; *Sq.*, squamosal; *Vo.*, vomer; *Zyg.*, zygomatic process of squamosal.

surpassed evolutionary changes in contemporary land dwelling carnivores. The future will show, I believe, that the geological history of the odontocetes and mysticetes is considerably longer than some investigators have conceded.

Returning to telescoping as a factor in the remodeling of the cetacean skull, we find that one of the earliest and most obvious results of this general evolutionary trend was the reduction and virtual elimination of the intertemporal region. This was not accomplished by the elimination of elements in the cranial region, but by the elongation of certain bones and the slipping of others over those with which they at one time met edge to edge in sutural union. In one group, the Odontoceti, there has been an elongation of the proximal portion of the maxillary and in the other, the Mysticeti, an elongation of the supraoccipital. In the first group there has been a backward overthrust of anterior cranial elements and in the second a forward overthrust of posterior cranial elements. While this general tendency in direction of the thrust prevails in most of the odontocetes under consideration, types also exist in which the backward and forward overthrusts are combined in such a way as to give rise to a more or less balanced condition of telescoping, such as is found in the physeteroids, while in the ziphioids the primary backward maxillary overthrust apparently was stopped abruptly by a final forward occipital thrust.

There is one fundamental difference in construction between the whalebone and the toothed-whale type of skull, and this feature may account for the different structural modifications that characterize these two living groups of cetaceans. In skulls of whalebone whales (Mysticeti), the maxillary can not overspread the braincase because its posterior extremity straddles the supraorbital process of the frontal in the form of two processes, the lower of which is known as the infraorbital and the upper as the ascending process. The upper surface of the expanded supraorbital process of the frontal is left bare and the relatively narrow ascending process of the maxillary is mortised into the body of the frontal behind the level of the narial passages. The infraorbital process of the maxillary lies beneath the anterior border of the inferior surface of the supraorbital process of the frontal and projects conspicuously behind and beneath the infraorbital foramen. It is quite obvious that any backward movement of the maxillary would be retarded by this interlocking with the supraorbital process of the frontal, but the impetus for telescoping was not to be blocked by any such impediment. Inhibited by what appear to be insurmountable obstacles at the base of the rostrum, the direction of the thrust was reversed from backward to forward. This forward overthrust of the elongate occipital shield carried the posterior and intertemporal elements forward, bringing the apex of the supraoccipital to or beyond the median interorbital level and forcing the parietal to override the frontal above the base of the supraorbital process, in some instances as far forward as the level of the proximal end of the nasal (*Balaenoptera acuto-rostrata*, *B. physalus*, and *B. borealis*).

In the toothed whale (Odontoceti) type of skull, as heretofore mentioned, the direction of the overthrust of the cranial elements has been mainly toward the rear. The entire proximal portion of the maxillary is pushed back over the supraorbital process of the frontal to meet or approach the supraoccipital at the level of or behind the orbit; laterally this bone spreads out and, together with the

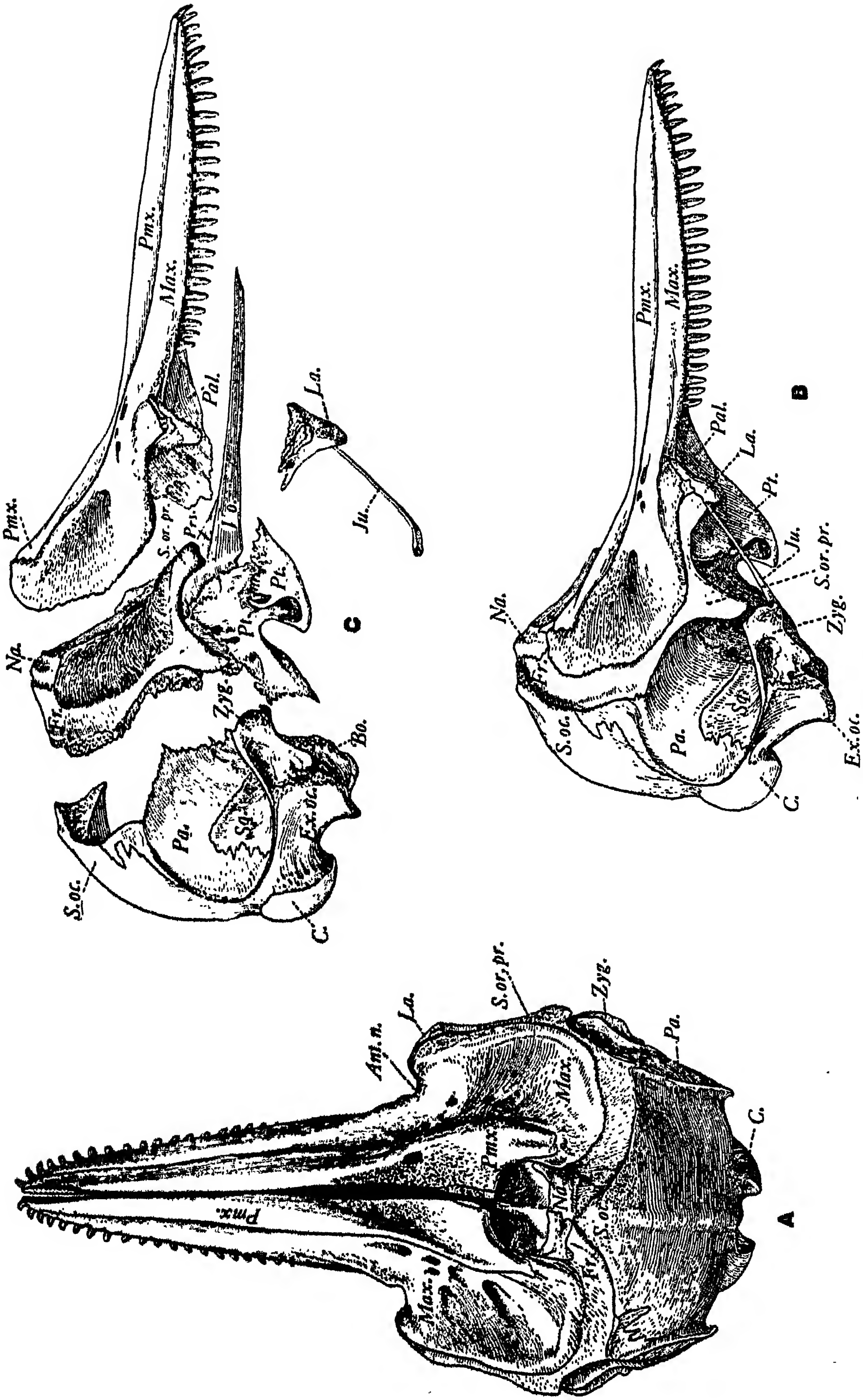


FIG. 3. SKULL OF TURSIOPS TRUNCATUS, HATTERAS, NORTH CAROLINA

A. Dorsal view. *B*. Lateral view. *C*. Lateral view of disarticulated skull, with braincase and rostrum detached.

thin underlying lateral plate-like extension of the frontal, forms a roof more or less complete over the temporal fossa. As viewed from the side the long axes of the frontal, parietal, and squamosal slope upward and backward, and give every appearance of having been crowded into their present position by some backwardly delivered force associated with the posterior overthrust of the maxillary. These opposite trends of thrust in the elements chiefly concerned in the telescoping process may be illustrated by the skulls of the bottlenose porpoise (*Tursiops truncatus*) and the Sei whale (*Balaenoptera borealis*).

Among the unusual conditions that have arisen through this telescoping process are the contact of the premaxillary with the supraoccipital (*Kogia*), the overriding of the palatine by the pterygoid and the contact of the latter with the maxillary (*Platanista*), the antero-posterior expansion of the alisphenoid and its contact with the supraoccipital (*Aulophyseter*), the backward projection of the lachrymal along the outer upper border of the supraorbital process of the frontal (*Xenorophus*), the outward extension of the facial portion of the premaxillary beneath the maxillary (*Xenorophus*), the sutural union of the external reduplication of the pterygoid with the squamosal (*Eurhinodelphis*, *Zarhachis*, *Platanista*, and *Stenodelphis*), the coalescence of the mesethmoid and ectethmoids to form a flattened bony plate on anterior wall of braincase over the greatly reduced frontal fontanelle (practically all living delphinoids), the wing-like lateral extension of the vomer which is applied to the ventral surface of the maxillary (young *Physeter*), the loss of the right nasal bone (*Physeter*), and the close approximation of the nasal bones with the supraoccipital (*Sibbaldus*). In the case of the blue whale (*Sibbaldus musculus*) portions of the nasal, premaxillary, maxillary, parietal, and frontal are present in one transverse plane. Rearrangements of the individual bones such as enumerated above are peculiar to the cetaceans and are the direct outcome of a remodeling of the skull.

ODONTOCETI

Small archaic toothed whales with skulls constructed along somewhat different lines from those of the zeuglodonts make their appearance toward the close of the Eocene. Their previous geological record is as yet unknown. If they were contemporaneous with the Middle Eocene and earlier Upper Eocene zeuglodonts, it seems surprising that their remains have never been found or at least identified among the many specimens obtained by the various parties that have explored the Fayum in Egypt. Other possibilities to be taken into consideration are that these archaic toothed whales may have been developing in some other part of the world or in fresh water, and that they first came into association with the zeuglodonts on the shores of the southern United States. Skulls of two of these small whales differing from one another in certain details of telescoping have been discovered in deposits approximately equivalent in time to those in which our North American Upper Eocene zeuglodonts were found. The braincases of these skulls are short and broad, quite compact, and less modified in some respects than in cetaceans occurring in later epochs. As compared with the zeuglodonts, they are noticeably contracted in a fore-and-aft direction. The individual bones in the skull as a rule are more ponderous than in the lighter constructed skulls of modernized porpoises.

These archaic toothed whales tried out a number of cranial modifications and long before their apparent extinction near the

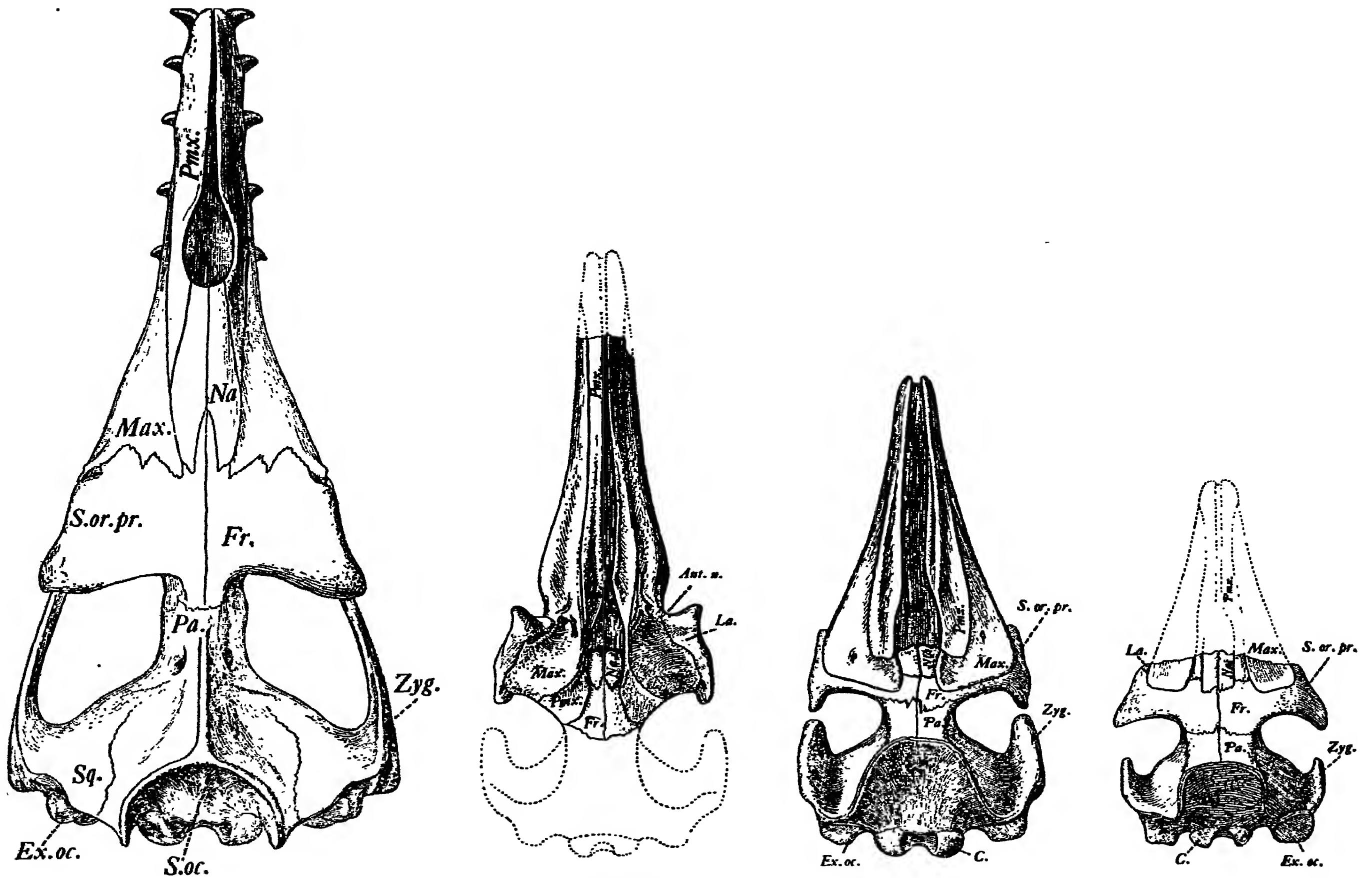
close of the Oligocene they had attained a high degree of specialization. The characters retained, especially in the skull and teeth, are primitive and not sufficiently diagnostic to connect them with any known species of zeuglodont, and the telescoping or remodeling of the skull is already so far advanced that the incipient stages of this general process are obscured by certain details of cranial construction.

One may visualize the steps in the transformation of a zeuglodont type of skull to that of the Eocene archaic toothed whale, but skulls demonstrating the actual stages have never been found. Assuming that the skulls of these archaic toothed whales have been derived from the zeuglodont type of skull, one must necessarily concede that the outer edge of the maxillary immediately in front of the supraorbital process of the frontal and the tooth-bearing portion of the maxillary, which projects backward beside the jugal below the orbit, must degenerate or be eaten away in order that the maxillary may be pushed back over the supraorbital process of the frontal. The jugal must lose its connexion with the maxillary and fuse to the ventral surface of the lachrymal bone. The lachrymal bone must continue to retain its position at the anterior margin of the supraorbital process of the frontal, but must be shifted so that it comes to lie on the ventral instead of the lateral face of the maxillary.

AGOROPHIIDAE

Skulls of the Upper Eocene genera *Xenorophus* and *Agorophius* conclusively show that the maxillary and premaxillary have been subjected to a backward thrust, which forced these bones over the supraorbital process of the frontal and carried the antorbital foramen backward until it came to lie near the level of the antorbital notch. These skulls, however, do not give us any clew as to how this slipping was accomplished. By referring to text figure 4 one can see at a glance in what respects the backward thrust of the proximal end of the rostrum has changed the relative positions of certain elements. In all known zeuglodont skulls the maxillary straddles the anterior face of the supraorbital process of the frontal in a manner comparable to that existing in the living whalebone whales (Mysticeti). Unless the infraorbital portion of the maxillary atrophied and finally disappeared with the reduction of the molar teeth, and we have no direct evidence to show that such was the case, no backward movement of the maxillary would be permitted.

In the case of *Xenorophus sloanii* (Kellogg, 1923), the maxillary is excluded from the orbital region by the combined jugal and lachrymal. The lachrymal bone has already assumed a position typical of toothed whales (Odontoceti), abutting against the anterior border of the supraorbital process of the frontal and mortised into the ventral face of the maxillary. Nevertheless, this bone differs from the lachrymal in all known porpoises in having an ascending process, which has overspread the outer upper border of the supraorbital process of the frontal. The remodeling of the skull has proceeded in directions that have not been followed by odontocetes of later geological stages. Some inexplicable peculiarity in the skull of an immediate precursor gave rise to unusual conditions in the *Xenorophus* skull, which differs from all other known cetaceans in having the premaxillary widened posteriorly so that it extends conspicuously outward underneath the maxillary over the basal half of the supraorbital process. Furthermore, the maxillary slopes very abruptly in front of the antorbital notches. Although the



Prozeuglodon stromeri *Xenorophus sloanii* *Agorophius pygmaeus* *Archaeodelphis patrius*

FIG. 4. DORSAL VIEWS OF UPPER EOCENE SKULLS

Prozeuglodon stromeri, Qasr-el-Sagha stage, Fayum, Egypt. *Xenorophus sloanii*, Ashley marl, South Carolina. *Agorophius pygmaeus*, Ashley marl, South Carolina. *Archaeodelphis patrius*, (?) Ashley marl, South Carolina.

skull of *Xenorophus* has a rather elongated rostrum, it differs from the zeuglodont skull in having the opening leading to the nostrils located behind the level of the anterior margin of the orbit. The nasal bones are noticeably shortened, and their bases are mortised into the frontals near the level of the posterior margin of the orbit. The palatine bones of this skull extend forward beyond the antorbital notches, and there is no evidence that their position with respect to other basicranial elements was affected to any marked extent by the backward thrust of the maxillary. The posterior extremity of each palatine abuts against the corresponding edge of the pterygoid and, unless they were permitted to slide under the latter, they would remain in approximately their original positions, but a telescoping of these elements has occurred in some of the living porpoises, for in *Mesoplodon* the palatines are largely overspread by the greatly enlarged pterygoids, while in *Platanista* the palatines are greatly reduced and are completely overspread by the pterygoids.

The idea that the skull of the Upper Eocene *Agorophius pygmaeus* (Leidy, 1869; True, 1907) bore some resemblance to the rorquals apparently originated with Paul Gervais (1871), and Cope (1895) remarked that if teeth were absent it would be necessary to refer this cetacean to the Mysticeti. The possibility that *Agorophius* may be one of the direct ancestors of the whalebone whales (Mysticeti) appears to be excluded, in view of the limitations imposed by the actual mechanical construction of the skull. In *Agorophius* the maxillary broadly overspreads the supraorbital process of the frontal and does not stop in front of or project backward beneath it, as in all known Mysticeti. On the contrary in skulls of both fossil and living whalebone whales the proximal end of the maxillary as seen from a dorsal view abuts against the supraorbital process of the frontal for most of its width, but is attached to the frontal in the interorbital region by a narrow ascending process. Once inaugurated it is difficult to conceive how the general process of telescoping could be reversed, since the backward slippage of the maxillary depends upon the removal of an obstruction consisting of the infraorbital portion of this bone, a process furthermore that is retained by all known whalebone whale skulls. Any assumption that the mysticete skull was derived from an *Agorophius* type necessitates a reversal of the impetus that led to the backward thrust of the proximal rostral elements in addition to a secondary development of an interlocking maxillary. To accomplish this the broad plate of the maxillary which already has overspread the supraorbital process must be reduced to a narrow ascending process and a broad infraorbital process must arise.

The association of *Agorophius* with the odontocetes rests on a much sounder basis, for this archaic toothed whale undoubtedly represents a somewhat distantly related precursor of the squalodonts, which include a number of diverse types. There is reason to believe that *Agorophius* at least represents a morphological stage through which the toothed whales may have passed in their development and that the subsequent remodeling of the odontocete cranium was accomplished by a forward movement of the occipital region until the supraoccipital shield came in contact with the frontals. Additional support to the view that the parietals were crowded out by some forward movement of the posterior elements is to be found in skulls of immature bottlenosed porpoises (*Tursiops truncatus*), in which the parietal bones form the outer upper border

of the so-called occipital shield and are broadly overspread by the supraoccipital.

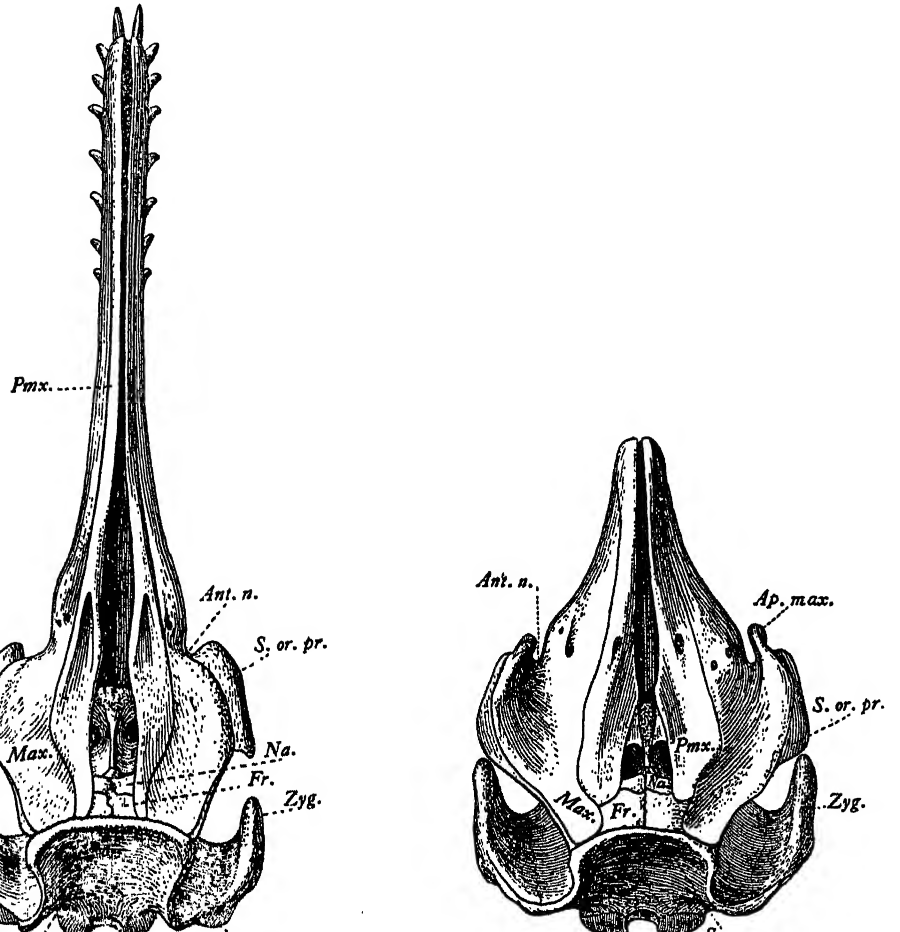
It would appear that the archaic toothed whales and the zeuglodonts, which had dominated the later Eocene seas, dwindled in numbers almost to the point of extinction by the close of the Oligocene. So far as the record shows, an extraordinary transformation of the odontocete skull took place in the interval of time preceding the beginning of the Miocene, which seemingly swept forward with prodigious rapidity, for several families had already acquired their peculiar details of structure by that time. Nevertheless one must not forget that the developmental history of the toothed whales during the Lower and Middle Oligocene is wholly unknown and that there is a surprising scarcity of described forms from the Upper Oligocene. The archaic toothed whales seem to have given rise to the squalodonts, which were the forerunners and perhaps the direct ancestors of the primitive ziphioid and iniid porpoises. These squalodonts continued through the Miocene, attaining their highest development, but perhaps not their greatest size. The sudden arrival of delphinoids with highly telescoped skulls as well as physeteroids with depressed braincase and characteristic postrostral basin in the Lower Miocene is the most startling evidence in favor of a rapid remodeling of the archaic toothed whale type of skull during the Oligocene, if it can be shown that they are derivatives of the later Eocene stock of true whales. One would hardly anticipate so radical a remodeling of a generalized type of skull in the course of one geological period.

The assemblage of toothed whales, which begin their career in the Lower Miocene, includes at least five of the recognized families of odontocetes. These families may be listed according to their specialization as follows: Squalodontidae, Iniidae, Ziphiidae, Delphinidae, and Physeteridae. Even in the skulls of these early Miocene porpoises the passages leading to the nostrils have been pushed backward to the level of the eyes and the choanae are nearly vertical, an adaptation for breathing in the water. The postorbital constriction has been eliminated on the skulls of all of these extinct porpoises, and the frontal bones are in contact posteriorly with the supraoccipital. The skulls of all known Miocene porpoises are constructed along the same general mechanical lines as those now living, although their rostra may assume quite different proportions. A noticeable tendency toward the lengthening of the rostrum is evidenced in many of the Miocene genera, and this process seems to culminate in the late Miocene or early Pliocene. Porpoises with moderately elongated rostra, actually much shorter than the peculiar Miocene porpoises hereinafter discussed, are found in the existing pelagic faunas, but it was not until the later Miocene that the true short-snouted porpoises made their appearance. The history of the several families of toothed whales may be traced briefly and the typical features of their respective groups illustrated by selected genera.

SQUALODONTIDAE

The oldest known faunas of pelagic mammals of the Lower Miocene appear to be those obtained from the Patagonian marine formation on the coast of Chubut Territory, Argentine Republic, and the sand pits of Libano and Bolzano, near Belluno, in the Province of Venetia, Italy. Among the peculiar types of extinct whales found in these formations are the shark-toothed porpoises, *Prosqualodon australis* (Lydekker, 1894), *Pho-*

berodon arctirostris (Cabrera, 1926), *Squalodon bariense* (Dal Piaz, 1916), and *Squalodon bellunense* (Dal Piaz, 1916). Porpoises of this type have been called squalodonts because of the general similarity between their teeth and those of sharks; but the teeth of squalodonts, unlike those of sharks, have two or three roots. These squalodonts must trace their ancestry back to unknown small archaic toothed whales of the Eocene, having teeth of similar shape and skulls of an antecedent construction. It is obvious that the narial passages have moved farther back than in their Eocene predecessors; the nasal bones are very much atrophied and are pressed into the frontals on the forewall of the braincase. In addition to other peculiarities possessed by these skulls, there are two small apertures on the anterior wall of the braincase for the passage of olfactory



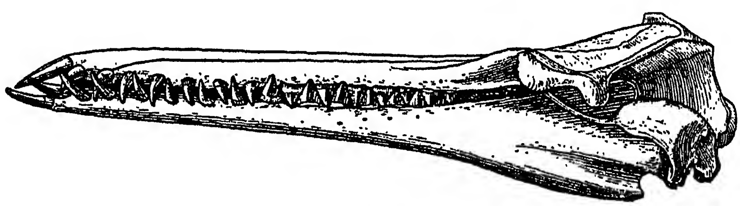
Squalodon calvertensis *Prosqualodon australis*

FIG. 5. DORSAL VIEWS OF SKULLS

Prosqualodon australis, Lower Miocene, Patagonia. *Squalodon calvertensis*, Middle Miocene, Maryland

nerves leading to the "blow hole apparatus." Similar foramina are present in all known squalodont skulls. In the progressive specialization and perfection of the squalodont skull during Oligocene time, the postorbital constriction was eliminated by the exclusion of the parietal bones from the vertex and the abutting of the frontal bones against the upper border of the supraoccipital. In the course of this telescoping process the backward overthrust of the maxillaries was continued until they met a barrier wall of bone, the crest of the supraoccipital. Hence in all known squalodonts the maxillaries are in contact posteriorly with the upper border of the supraoccipital and cover the underlying lateral extensions of the frontal bones.

Prosqualodon had 14 teeth in each upper jaw and hence the total complement of teeth would number 56, if the lower teeth, which are not known, equal the upper. The 3 incisor teeth are lodged in the premaxillary bone as in other squalodonts. Briefly stated this genus is characterized by maxillaries extending backward beyond the premaxillaries and abutting against the supraoccipital, a short broad rostrum, a deep mesorostral trough, narial passages nearly vertical, passages for olfactory nerves separated by mesethmoid, combined lachrymal and jugal wedged in between maxillary and anterior margin of supraorbital process of frontal, robust zygomatic processes, relations of pterygoids and palatines similar to *Globicephala* but less telescoped, pterygoids forming a sinus on each side in front of choanae but without external reduplication, heterodont dentition, and the symphysis of the mandible extending backward to the level of the sixth tooth counting forward from the last. Curiously enough these short beaked squalodonts appear to be restricted to the Southern Hemisphere, where they have been found in association with the more widely distributed long-beaked types. Several fairly well preserved skulls of *Prosqualodon australis* have been collected in Patagonia. An exceptionally well preserved skull of another species, *Prosqualodon davidi* was recently discovered at Wynyard, Table Cape, Tasmania.



Squalodon bariense

Fig. 6. Lateral View of Skull of Squalodon bariense, Middle Miocene, France

The tendency of cetaceans descended from the same stock to diverge in character as they become specialized is well illustrated by the short-beaked and long-beaked porpoises which comprise the family Squalodontidae. Inasmuch as these squalodonts were already differentiated into at least three distinct series at the dawn of the Lower Miocene, their predecessors must have flourished in the Oligocene seas, yet the family appears to have had but one survivor in the Pliocene pelagic faunas. Very little is known in regard to the geographic distribution of the series typified by *Prosqualodon* and *Neosqualodon*, yet *Squalodon* and its relatives are known to have had a very extensive

distribution. *Prosqualodon* is the best known member of the short-beaked series. *Phoberodon* and *Squalodon* may be taken as typical representatives of the least specialized long-beaked series, while *Neosqualodon* with its elongated rostrum and excessively increased dentition undoubtedly represents the most highly specialized series.

The relations of the cranial bones in all of the long-beaked squalodonts belonging to the *Phoberodon-Squalodon* series appear to be essentially the same, and they differ from one another merely in certain minor details. The slender rostrum is nearly twice as long as the braincase. The backward thrust of the rostrum has carried the maxillary over the frontal considerably beyond the level of the orbit, and its posterior edge abuts against the supraoccipital. The frontals, which lie underneath the maxillaries, are also in contact posteriorly with the supraoccipital, and the parietals are excluded from the vertex of the skull. The mesethmoid divides the frontal fontanelle into two orifices, provides additional support for the vertex of the skull, and forms a thin veneer of bone around the dorsal and lateral faces of the presphenoid between the narial passages.

For *Phoberodon arctirostris* (Cabrera, 1926) of the Lower Miocene Patagonian marine formation of Chubut, a skull and nearly complete skeleton are known. The telescoping of the braincase and the contours of the entire skull are similar to *Squalodon*, but the zygomatic processes are much more robust. If the presence of rudimentary basal cusps on the penultimate maxillary molar and the two posterior mandibular molars has any deep seated significance, the dentition of *Phoberodon* must be considered as more primitive than that of *Squalodon*. Cabrera contends that the dental formula of *Phoberodon* should be written as follows: I. 3/3; C. 1/1; Pm. 6/6; M. 5/3 = 56. It is at least certain that this squalodont had 11 trenchant cheek teeth in each upper jaw and 9 in each lower jaw. The high and rather narrow scapula has a large broad acromion and a small coracoid process. The humerus has assumed the peculiar form of living odontocetes. The cervical vertebrae are free. The vertebral column is incomplete, but Cabrera concluded that this porpoise must have had 7 cervical, 9 dorsal, 12 lumbar, and 18 or 20 caudal vertebrae.

The genus *Squalodon* first makes its appearance in the upper division of the Lower Miocene in Italy near Belluno, where two species have been recognized. According to Dal Piaz (1916), *Squalodon bariense* with 58 teeth occurs only in the lower level of the Upper Langhian stage and the second species, *Squalodon bellunense*, with 56 teeth in the upper level. The teeth of *Squalodon* are increased above 44, the typical eutherian number, and consequently have been the subject of varying interpretations. Dal Piaz contends that 8 or 9 of the cheek teeth are premolars and that the molars may vary from 1 to 3. On the other hand, Van Beneden, Zittel, and others have interpreted the cheek teeth as comprising 4 or 5 premolars and 5 to 7 molars. Whatever may be the correct interpretation of the dental formula, the cheek teeth in the upper jaw of *Squalodon* are known to vary from 10 to 12 and in the lower jaw from 9 to 11. At least 62 teeth were present in the skull of *Squalodon zitteli* (Paquier, 1894; Zittel, 1876–77), a Middle Miocene species found in the neighborhood of the village of Bleichenbach in lower Bavaria. This squalodont had 12 cheek teeth in each upper jaw. This is especially interesting in view of Winge's suggestion (1921, p. 24) that the increase in cheek teeth above the typical number 7 might

have been produced by the intercalation of 4 milk teeth in the series, if they were found not to exceed 11. The Miocene genus *Squalodon* (Kellogg, 1923) with its telescoped and shortened braincase, limited facial depression, large temporal fossae, heterodont dentition, and elongated mandibular symphysis, is not uncommon in European and North American formations of Middle and Upper Miocene age. Their skulls measured about 3 feet in length, and according to our present knowledge these squalodonts scarcely attained a length of 16 feet.

The slender-beaked *Neosqualodon assenzae* (Dal Piaz, 1904; Gemmellaro, 1921) represents one of the odontocete extremes in the increase and elaboration of a heterodont dentition. This extinct porpoise was a member of the pelagic fauna of the upper division of the Langhian stage of the Lower Miocene and has been found at two localities in Sicily. Fortunately the left side of the skull and the left mandible found in an asphalt pit in the Tabuna region near Ragusa, province of Siracusa, Sicily, are sufficiently complete for the determination of the dental formula. It is certain that *Neosqualodon* has 3 incisors and 1 canine tooth in each jaw, and that there are 26 cheek teeth in the mandible. The skull was then furnished with something like 120 teeth. Each of the 10 posterior teeth in the mandible has one or more accessory cusps on the anterior and posterior cutting edges. Some of the lower teeth have as many as four accessory cusps on the anterior cutting edge. At least 7 of the posterior maxillary teeth are serrated on both cutting edges. The rostrum and mandible are unusually elongated, and the rostrum is fully three times as long as the braincase. The braincase, so far as known, is similar to *Squalodon* with the narial passages moved backward beyond the level of the preorbital angles of the supraorbital processes. The lachrymal and the jugal with its long styliform process are likewise similar. The skull of *Neosqualodon* measures about 21 inches in length. The subsequent history of this series is unknown.

The Miocene squalodonts seem to represent a line of development that was neither antecedent to any group of modernized porpoises nor adapted to environmental conditions of the Pliocene. A late survivor, *Prionodelphis rovereti* (Frenguelli, 1922), occurs in the estuary facies of the Lower Pliocene Parana formation in the province of Entrerios, Argentine Republic. Judging from their shark-like teeth, these squalodonts were well adapted for a predaceous life, and hence could secure an adequate food supply wherever fish or small pelagic mammals were present in sufficient numbers to insure easy capture. Unless the prevailing pelagic conditions were radically different during the Miocene than at present, their distribution should correspond in a general way with that of the living killer whale (*Orcinus*). Remains of squalodonts have been found in Europe, North America, South America, New Zealand, and Australia.

INIIDAE

Our knowledge of the Tertiary history of the iniids is most unsatisfactory, resting as it does upon a few imperfectly preserved fragments of skulls of Miocene and early Pliocene age. The teeth of these iniids have lost their heterodonty, and their cranial characters imply as long a geological history as any of the extinct porpoises associated with them during Miocene time.

Proinia patagonica (True, 1909), which was based on an imperfect crushed skull and a single cervical vertebra obtained from the Lower Miocene Patagonian

marine formation at Darwin Station, Santa Cruz Territory, Argentine Republic, is in many respects quite specialized. The relationships of *Proinia* are somewhat doubtful, for the structures needed for definite classification, such as the arrangement of the bones below the choanae and the maxillaries, are missing. Cabrera (1926) has recently suggested that these remains belong either to *Diochotichus* or to a closely related genus. It is obvious that it is much larger and quite distinct from either *Inia* or *Lipotes*. As compared with *Inia*, it is less specialized in having a larger exposure of the frontals on the vertex, more nearly vertical and less forward sloping narial passages, and supraorbital processes with less elevated extremities. The skull of *Proinia* presents the following characters: abruptly elevated vertex formed by large rectangular median portions of frontals, narrow supraorbital processes of frontals directed obliquely forward, orbit anteriorly situated, large temporal fossae bounded above by strong ridges or crests, outer wall of braincase convex, and zygomatic process convex externally with well developed postglenoid process. Granting that *Proinia* is a true iniid we must look further back in geological time for the progenitors of this family, for contemporaneous squalodonts were highly specialized and well established in the early Miocene. Abel, Winge, Miller, and others have construed the available data as showing that the iniids, if not closely related, at least lean toward the squalodonts.

A section nearly 8 inches in length of the symphysial region of the mandibles, with six pairs of alveoli and without longitudinal external furrow, which was found associated with four loose teeth in the upper San Pablo formation near Rodeo, California, formed the basis for *Hesperocetus californicus* (True, 1912). This late Upper Miocene porpoise has been referred to the Iniidae chiefly on account of the conformation of the symphysis and the shape of the teeth. The teeth have slightly recurved crowns covered with rugose enamel in addition to a longitudinal postero-internal carina and an antero-external carina. The teeth are further characterized by the lack of a distinct cingulum, the absence of an enlarged protocone shelf, and the imperceptible constriction of the root below the crown. They are separated by wide interspaces, those of the upper jaw fitting in between those of the lower jaw and vice versa when the jaws are shut, and their apices rest in the interalveolar depressions.

Another extinct porpoise, *Saurodelphis argentinus*, with iniid affinities occurs in the Lower Pliocene Parana formation of the Argentine Republic. The original material, consisting of two fragments of a mandible collected by Montes de Oca on the shore of the Parana River, was described and figured by Burmeister in 1871. Subsequently (1891), Burmeister erroneously referred an incomplete skull of *Ischyrorhynchus vanbenedeni* to *Saurodelphis argentinus*, and as a result of this mistaken allocation the affinities of this fossil porpoise were misinterpreted for many years. The larger fragment of the type specimen, which consists of a portion of the symphysis with 6 teeth and 6 empty alveoli on the left side, and 3 teeth and 4 empty alveoli on the right, is 15 inches long, and its greatest height is 2.5 inches. A distinct furrow, beginning at the posterior end of the symphysis and extending forward to near the extremity, traverses the lower border of the external face. The alveoli are elliptical, and behind and anterior to each is a small circular depression placed outside of the alveoli instead of in line with them, apparently

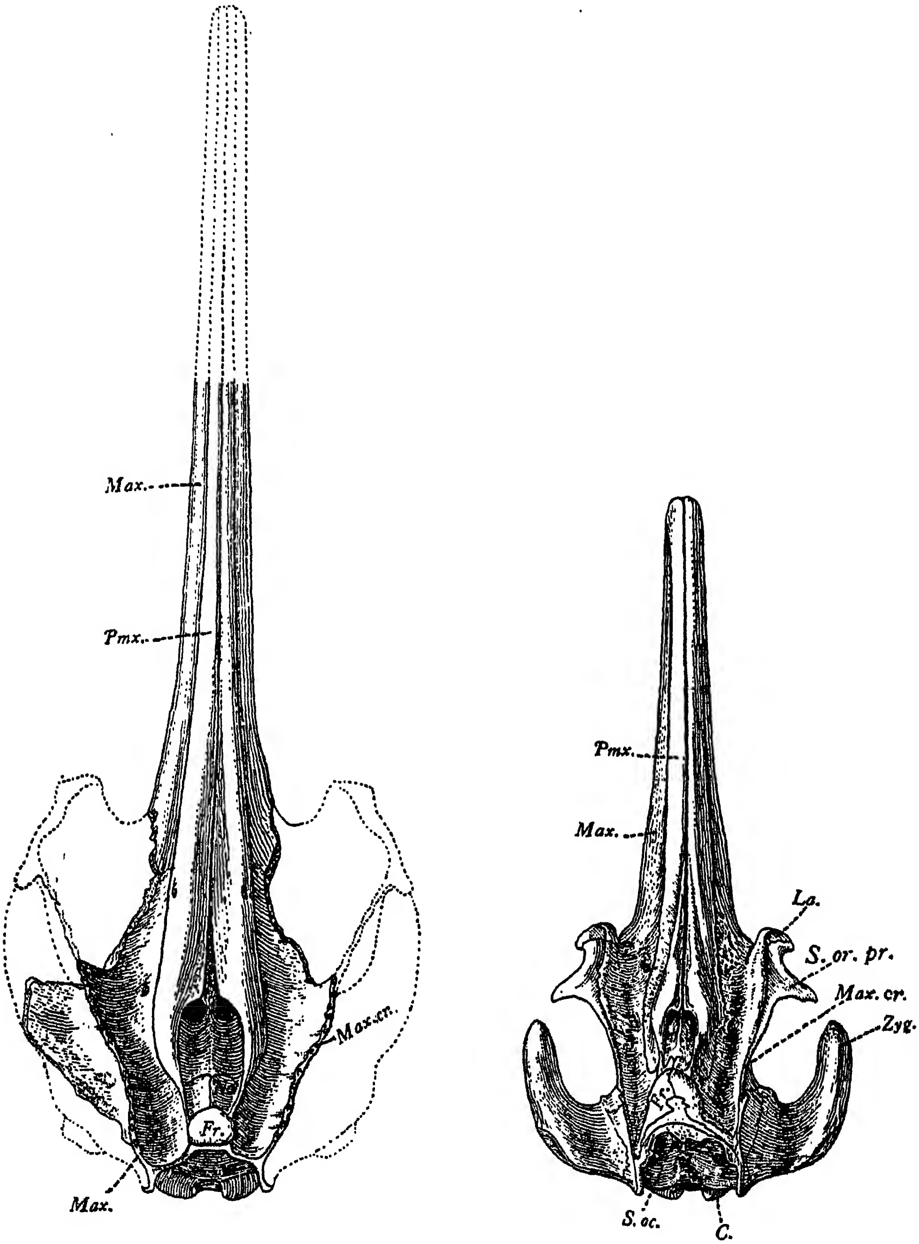


FIG. 7. DORSAL VIEWS OF SKULLS
Ischyrorhynchus vanbenedeni, Lower Pliocene, Parana, Argentine Republic. *Inia geoffrensis*, Santarem, Brazil

marking the position of the apices of the upper teeth when the jaws are shut. The teeth are large, compressed, and not closely approximated, with acute conical crowns covered with rugose enamel. Between the base of the crown and the

neck of the root is a well marked cingulum. The root is gibbous below the neck. Some of the teeth have the extremity of the root irregularly divided into three branches. The smaller teeth resemble the anterior teeth of the living South American genus *Inia* in the shape of the crown, the cingulum, and the compression of the distally expanded root. None of these teeth exhibit the distinct internal protocone shelf that is so characteristic of the crown of posterior teeth of *Inia*.

In 1891, Burmeister described and figured an imperfect skull collected by Artemio Carreras at La Curtiembre, near Parana, Argentine Republic. In restoring this skull, Burmeister used the living *Stenodelphis* as a model and added the end of the rostrum of another porpoise. This composite specimen was erroneously referred to *Saurodelphis argentinus*, as has already been pointed out by Abel (1909) and Rovereto (1915). Burmeister was the first to suspect that this extinct porpoise might be identical with *Ischyrorhynchus vanbenedeni*, but it remained for Cabrera (1926) to allocate the skull to that genus and species. This strongly telescoped Lower Pliocene porpoise skull differs from all known iniid skulls in having the zygomatic processes placed far forward, and the maxillaries are pushed farther back toward the occiput. The outer borders of the maxillaries in the supraorbital and supratemporal regions are strongly bent upward, recalling *Platanista* in some respects. Doubtless a certain resemblance exists between *Ischyrorhynchus*, *Inia*, and *Platanista*, but not a close one. It is obvious that the lateral crests of the maxillaries were much higher than in *Inia*, and it is possible that when complete they may have resembled those of *Platanista*. The inclination of the posterior wall of the narial passages is much less steep than in either *Inia* or *Platanista*, and the small, conspicuously elevated vertex is formed by the frontals. Although both nasal bones are missing, the cavities in which they were lodged are distinct enough to determine their proportions, and it is fairly certain that they were pressed against the frontals on the posterior wall of the narial passages. The irregularly spaced teeth are large, elliptical in section; the crowns of the teeth are conical and low, with apex slightly recurved backward, and covered with rugose enamel. The roots of the teeth are thickened, and the anterior teeth are strongly inclined forward. The imperfect skull, which lacks the end of the rostrum, has a length of about 25 inches and was nearly 13 inches in breadth across the zygomatic processes when complete, while a large complete skull of *Inia* has a length of but 21 inches and a zygomatic breadth of 9½ inches.

Skulls of living river porpoises of the family Iniidae differ from all other odontocetes in having a more or less fenestrated, freely projecting, fortuituous process of the maxillary, extending backward outside of the sinus in front of the choana to or beyond the level of the sphenoid fissure. The South American *Bouto* (*Inia geoffrensis*) and the Chinese *Peh Ch'i* (*Lipotes vexillifer*), now living in Tung Ting lake and its tributaries, are porpoises of small or moderate size whose skulls have elongated rostra; narrow facial depression with external borders of maxillaries bent upward; maxillaries extending forward to extremity of rostrum; orbits situated in front of level of narial passages; nasals flattened up against frontals on anterior wall of braincase, contributing upper border of posterior wall of narial passages and overspread inferiorly by mesethmoid; elevated vertex; elongated zygomatic processes; palatine forming part of anterior wall of narial passage and separated

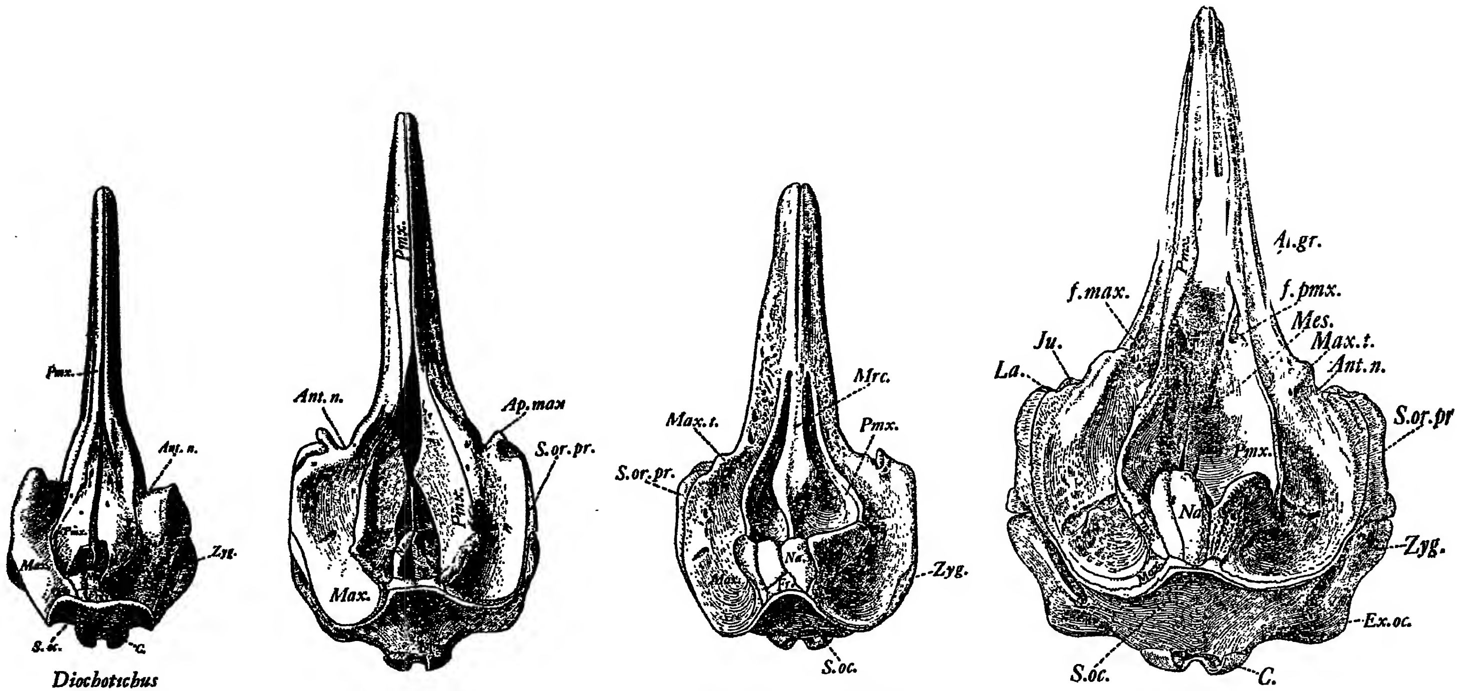
from its mate on median line of palate by axial ridge of vomer; simple pterygoids neither spreading laterally over alisphenoid nor reduplicated along either margin, and not completely covering palatines on ventral aspect of skull; long mandibular symphysis; and numerous teeth in both jaws, but those in the upper jaw lodged solely in the maxillaries. The crowns of the teeth are covered with nodular or reticulate enamel and are anteroposteriorly compressed; the roots are laterally compressed and expanded distally. The teeth of *Inia* have a large internal protocone shelf covered with rugose enamel, while those of *Lipotes* have this portion of the tooth very much reduced. The cervical vertebrae are all free.

ZIPHIIDAE

In addition to the squalodonts there occurs in the Lower Miocene Patagonian formation a peculiar extinct porpoise *Diochotichus vanbenedeni*, which possesses so many anomalous features that its relationships were somewhat of a puzzle for many years. Moreno (1892), the original describer, did not reach any conclusion as to its family position. Lydekker (1894) considered it to be a primitive platanistid, and True (1910) thought that it was a squalodont with simple, single-rooted, conical teeth. Dal Piaz (1916) made a new family, Squalodelphidae, for the reception of this porpoise and an allied cetacean, *Squalodelphis fabianii*, found in the Upper Langhian stage of Belluno, Italy. More recently Winge (1918, 1921) and Cabrera (1926) have considered *Diochotichus* to be the most primitive known form of the beaked whales (family Ziphiidae). Four more or less complete skulls of this peculiar ziphioid whale have been collected in Chubut and Santa Cruz Territories, Argentine Republic.

The skull of *Diochotichus* is characterized as follows: 23 teeth in each maxillary and 19 in each mandible; posterior teeth are short, with single main cusp, covered with smooth enamel, and have an anterior and posterior minute tubercle; anterior teeth are conical, long, and curved; all the teeth are single rooted; premaxillary expanded anteriorly and not touching posteriorly upon the frontal; maxillary bent upward behind premaxillaries, with its inner margin on a level with the vertex and in contact posteriorly with crest of supraoccipital; nasal bones large, not overhanging narial passages; large olfactory foramina separated mesially by mesethmoid; low broad supraoccipital; backward extension of posterior margin of temporal fossa; zygomatic processes large, thick, oblong, and very little divergent; elongate sinus on ventral surface of maxillary anterior to choana; pterygoid with an inner vertical plate and an outer more or less horizontal plate, which conceals the alisphenoid; mandibular symphysis long; mandible strongly convex posteriorly; and length of skull 23 to 25 inches. The facial depression is farther forward than in living ziphioids, but is clearly antecedent to the postrostral depression seen on skulls of living beaked whales, while the elevation of the vertex is what might be expected in a precursor of the more highly specialized types of the later Miocene. The cervical vertebrae are free, and as True pointed out the characters exhibited by the vertebral column are distinctly ziphioid.

It shares with *Squalodon* the following important characters: orbital plates of maxillaries do not completely cover the supraorbital processes of the frontals; vomerine trough wide; zygomatic processes large, thick, and oblong; long mesethmoid separating the olfactory foramina; and premaxillaries expanded anteriorly



Diochotichus vanbenedeni

Mioziphius belgicus

Choneziphius planirostris

Ziphius cavirostris

Fig. 8. Dorsal Views of Skulls

Diochotichus vanbenedeni, Lower Miocene, Patagonia. *Mioziphius belgicus*, Upper Miocene, Belgium. *Choneziphius planirostris*, Upper Miocene, Belgium. *Ziphius cavirostris*, Newport, Rhode Island.

and abbreviated posteriorly. The relations of the bones on the ventral surface of the skull are quite different from conditions in the iniids.

Squalodelphis differs from *Diochotichus* in the following particulars: antorbital maxillary protuberance slightly more accentuated; rostrum narrower at base; maxillary almost wholly concealed at base of rostrum by overlying premaxillary; 15 teeth in each maxillary and mandible; posterior teeth unicuspid, compressed, bicarinate, and acuminate, and covered with rugose enamel with a cingulum formed by rugosities on internal side at base; length of skull about 25 inches; symphysis one half total length of mandible.

A distinctly modernized ziphioid, *Mioziphius belgicus* (Abel, 1905), which is not so distantly related to living beaked whales, was a member of the Upper Miocene pelagic fauna of the Belgian coast. Its skull is slightly larger than that of the living *Mesoplodon*. It is rather ponderous and slightly asymmetrical. It has the thick extremities of the premaxillary bones bent upward opposite the nasal bones; the olfactory foramina are open even in old individuals; large prenarial fossa; no mesorostral ossification; maxillaries strongly swollen in front of antorbital notches; premaxillaries in contact on distal half of rostrum, completely concealing vomerine trough; maxillary with 37 to 48 closely approximated alveoli, but with intervening septa almost entirely obliterated, giving rise to a broad shallow alveolar gutter. The mandibles have a short symphysis, about one-fourth the length of the rostrum, and are furnished with two pairs of large functional teeth, of which the anterior or terminal pair is the larger. These teeth are lodged in projecting sockets formed of cancellous bony tissue. The mandibular dentary groove is narrow, shallow, and reduced posteriorly. With the exception of the two pairs of mandibular teeth, the others, if present, were lodged in the gum.

The ziphioid genera *Mioziphius*, *Choneziphius*, and *Ziphius* are a direct outcome of a peculiar arrangement of the bones that enter into the composition of the vertex of the cranium. We have seen that the vertex was somewhat raised in the Lower Miocene genera *Diochotichus* and *Squalodelphis*, and that the premaxillaries were blocked off posteriorly by the raised crest-like postero-internal margins of the maxillaries. Any additional backward thrust of the maxillaries and premaxillaries would elevate the posterior extremities of these bones, for the maxillaries were in contact with the crest of the supraoccipital in these Lower Miocene ziphioids. Partly in this manner and partly by actual bony outgrowths, the skulls of these Upper Miocene ziphioids acquired their peculiar elevated vertex overhanging a large bowl-shaped postrostral depression.

The skull of *Choneziphius planirostris* (Cuvier, 1836; Capellini, 1885; Weber, 1917) is somewhat unusual in that it is the only Upper Miocene ziphioid known to have a premaxillary that retains distinct vestiges of alveoli, notwithstanding the probability that if teeth were present in the upper jaw they were lodged in the gum. This extinct ziphioid, or closely related species, occurs in the Upper Miocene sands of the Antwerp Basin, the Edisto marl of South Carolina, the Pliocene Red Crag of Suffolk, England, and the Pliocene sands near Siena, Italy. This ziphioid skull is distinguished by having an attenuated rostrum not noticeably widened at the base, but somewhat swollen and thickened near the middle; form of rostrum subject to age, individual, and perhaps sexual variations; prenarial

fossa formed by the ankylosed premaxillaries, which develop an oblique sinistral crest along their line of contact, dividing the fossa into a large right cavity and a smaller left cavity; premaxillaries either closely approximated on the median line anterior to prenarial fossa or completely fused in old individuals; although concealed from view the narrow vomerine canal remains open; maxillaries not developing antorbital tuberosities; antorbital notch double; olfactory foramina large; mesethmoid thoroughly ossified; posterior extremities of premaxillaries bent upward behind the narial passages, forming the lateral borders of the high vertex; nasal bones reduced and lodged in deep fossae, which encroach upon premaxillary crests; lachrymal fused with frontal, maxillary, and jugal; maxillary and premaxillary with narrow alveolar gutter; vestigial septa between alveoli not visible on many specimens; length of skull in two old individuals about 27½ inches when complete.

Inasmuch as there are ten recognized living species of the genus *Mesoplodon*, there can be no objection to the assumption that species of these ziphioids were equally if not more numerous in preceding geological periods. Remains of extinct species of *Mesoplodon* are rather common in the Upper Miocene sands of the Antwerp Basin (Abel, 1905), the Edisto marl of South Carolina (Leidy, 1877), the Red Crag of Suffolk, England (Owen, 1870), and the Pliocene deposits of Italy (Vigliarolo, 1894). Unfortunately the majority of the fossil specimens referred to this genus consist solely of rostra, which are subject to age, individual, and sexual variations. Some of these specimens differ very little from living species, and one of them, *Mesoplodon longirostris* (Cuvier, 1836) may have been a precursor of the living beaked whales, *Mesoplodon bidens* and *M. europaeus*.

The palaeontological evidence bearing on the ancestry of the ziphioids indicates that they were derived from ancestors with functional teeth in both jaws. In the course of geological history the maxillary teeth have been suppressed except for the not infrequent occurrence of vestigial teeth buried in the gums, the symphysis of the mandible has been shortened, and the mandibular teeth have been reduced to one or two pairs. One of the distinctive features of living ziphioid whales is the presence of distinct jugal and lachrymal bones. The normal mammalian relationships of the jugal and lachrymal are transposed, for the former comes to lie in front of the latter on the ventral aspect of the skull. Living ziphioids retain a remnant of the dentary groove, which in some species consists of a longitudinal basirostral groove beginning in a blind pit below the antorbital maxillary tuberosity and extending forward along the side of the rostrum. As many as 17 to 19 vestigial maxillary teeth have been found in the gums of *Mesoplodon grayi* (Oliver, 1922). The antorbital maxillary tuberosities become by further enlargement the enormous longitudinal crests of *Hyperoodon rostratus* (Harmer, 1924). The rostrum has been deepened and solidified by ossification of the mesorostral cartilage. Some of the remarkable alterations that take place in the ossification of the rostrum during growth have been described by Forbes (1893). All of the living ziphioids (True, 1910) exhibit the same peculiar twisting, forward curling, and elevation of the posterior extremities of the premaxillaries and the maxillaries. The freely projecting nasal bones come to overhang the narial passages. The median portion of the supraoccipital bone has been raised higher to conform to the unusual elevation of the vertex. Another peculiarity is that the grooved anterior process of the periotic is lodged in a

slender ventrally directed dactyloid process of the squamosal. The unusual size of the air-sac at the outer side of the pterygoid, which is shaped to fit it, is another peculiarity of modernized ziphioid skulls. The base of the pterygoid has spread laterally, covering or nearly covering the alisphenoid bone, but the external reduplication is reduced to a low ridge. The cervical vertebrae tend to ankylose with one another. The dorsal, lumbar, and caudal vertebrae have high neural spines for the huge muscle masses associated with the caudal flukes. The wrist and finger bones are relatively small.

It would appear that the Lower Miocene ziphioids stand nearer to the squalodonts than to the sperm whales. In the past the beaked whales have been regarded as near relatives of the physeteroids, a conception which is disputed by Miller (1923), who calls attention to important morphological differences, such as the relation of the pterygoids to the palatines, and the structural features of the vertex.

DELPHINIDAE

The obliteration of the postorbital constriction by the exclusion of the parietals from the vertex and the accompanying contact of the supraoccipital with the frontals was brought about by a crushing together of the anterior and posterior elements of the skull. This stage of telescoping was fully established in the odontocetes of the Lower Miocene.

Scarcely less interesting than the foregoing is the fact that the maxillary had already reached its extreme posterior extension in the squalodonts *Phoberodon* and *Prosqualodon*, the ziphioid *Diochotichus*, and the delphinoid *Argyrocetus*. In all of these Lower Miocene South American porpoises the orbital cavity and the temporal fossa are roofed over by two flattened plates of bone, the uppermost being the maxillary and the lowermost the lateral extension of the frontal. The temporal fossa has not suffered any marked reduction because of any actual increase in size of the braincase. In only one of the preceding genera, *Diochotichus*, do the nasal bones retain a trace of their earlier function of providing a roof for the nasal cavity. What is of greatest interest, however, is the entire absence of any indication of heterodonty in these ziphioid and delphinoid types, and the fact that the premaxillaries project anteriorly beyond the maxillaries in all of these extinct porpoises. All of these genera, without exception, show that the narial passages have been forced backward against the anterior wall of the braincase and that their inclination is determined by the contour of this surface.

According to Miller (1923) the family Delphinidae comprises five distinct subfamilies, which he designated as follows: Delphininae, Eurhinodelphininae, Stenodelphininae, Delphinapterinae, and Monodontinae. The validity of the subfamily Eurhinodelphininae is somewhat doubtful, for it includes extinct porpoises in which the premaxillary is said to have been lengthened so that it projects conspicuously in front of the maxillary for a distance equivalent to one-fifth of the total, a condition that is not apparent in American specimens determined as *Eurhinodelphis*. The long beaked Lower Miocene porpoise *Argyrocetus* has been referred to this group by Cabrera (1926). As a general rule among more recent delphinoids the extreme tip of the premaxillary tends to lose its position on the ventral face of the rostrum because of the forward extension of the underlying maxillaries, and the teeth which were originally implanted in it are lost. A wide variety of extinct and living porpoises (True, 1889) are included in the

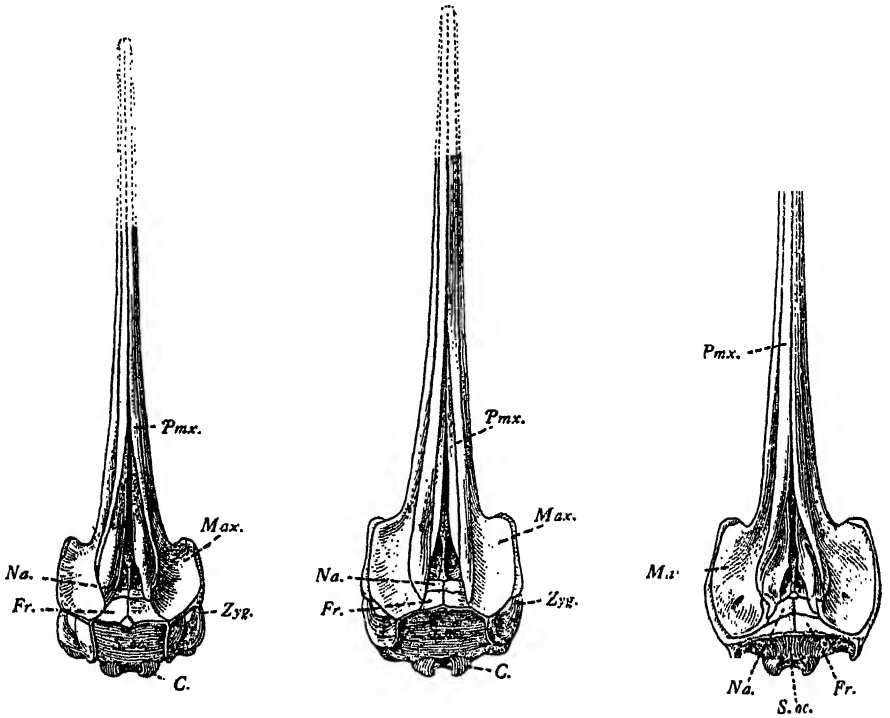
family Delphininae, ranging in antiquity from the Lower Miocene to the present time. Extinct relatives of the Stenodelphininae are not known with certainty earlier than the Lower Pliocene. The subfamilies Delphinapterinae and Monodontinae have a shorter geological history, the occurrences being restricted to the Pleistocene. One of the most remarkable features of the odontocete skull is its plasticity, which not only permitted a reshaping of its contours in conformity with environmental conditions imposed upon it, but also in some instances seemingly followed capricious paths of development. The rostrum may be either lengthened as in *Cyrtodelphis* or broadened as in *Globicephala*, but it is never deepened or solidified in the delphinoids.

Porpoises with long slender rostra predominated in the pelagic faunas of the Lower Miocene, as is evidenced by the occurrence of *Argyrocetus* in Patagonia, and *Ziphiodelphis*, *Cyrtodelphis*, *Eoplatanista*, and *Acrodelphis* in Italy. The occurrence of one little known, supposedly rather short-beaked porpoise, *Protodelphinus*, near Belluno was mentioned by Dal Piaz in 1922. The skeleton of another short-beaked porpoise, *Delphinavus newhalli* (Lull, 1914), measuring about 5 feet in length, has been found in the Lower Miocene Vaqueros formation of San Luis Obispo County, California. The skull is eleven and a half inches long, three-fifths of which is taken up by the rostrum. The mandibular symphysis is relatively very short, equivalent to slightly more than one-eighth of the total length of either ramus. It is interesting to note that the premaxillary bone is toothless and that the total complement of teeth is considerably increased above the normal, there being at least 180 teeth present. The teeth are all alike, with slightly recurved conical crowns covered with smooth polished enamel and no indication of carinae. The cervical vertebrae are separate, and there are at least 12 rib-bearing vertebrae. The fore limb or pectoral flipper is essentially delphinoid, with modified carpal bones and the usual arrangement of the metacarpals and phalanges in the digits. From some such type of extinct porpoise as this have descended the living porpoises *Delphinus* and *Prodelphinus*. In attempting to follow out this subject of the late Tertiary history of the delphinoids many equally interesting types of extinct porpoises must be omitted, and the interested reader is referred to the bibliography for references to these species.

As with many other groups of extinct mammals, we have an imperfect knowledge of the earlier Tertiary history of the long-snouted porpoises, which had already reached the fulness of their development in the Lower Miocene. They were then associated with several types of undoubtedly carnivorous squalodonts, but outlived most of them to find companions in the even longer-snouted extinct porpoises of the Upper Miocene. Whatever their previous geological history may have been, we are confronted in the Lower Miocene with a highly telescoped delphinoid type of skull, in which the backward overthrust of the maxillary was stopped by the crest of the supraoccipital and the rostrum conspicuously elongated. The splitting up of these long-snouted porpoises into several series had already commenced in the Lower Miocene, and each of these phyla, as we shall presently see, followed from then on their own peculiar path of development. A brief history of three of these series follows.

The first to be considered is taken to include the Lower Langhian *Argyrocetus*, the Upper Langhian *Ziphiodelphis*, and the Middle and Upper Miocene *Eurhinodelphis*.

This series includes porpoises with very long rostra, whose distal extremities are edentulous, or if teeth were present they were implanted in a dentary ligament along the vestigial alveolar groove. A somewhat damaged skull, nearly complete mandibles, including most of the symphysis, four cervical vertebrae and tion has been eliminated and the backward rostral thrust has carried the maxillary to the supraoccipital. The full complement of teeth exceeds 200. The vertex is limited to a narrow strip of the conjoined frontals, into the anterior borders of which the squared nasal bones have sunk. Cabrera (1926) has pointed out the great



Cyrtodelphis sulcatus *Argyrocetus patagonicus* *Eurhinodelphis bossi*

FIG. 9. DORSAL VIEWS OF SKULLS

Cyrtodelphis sulcatus, Lower Miocene, Italy. *Argyrocetus patagonicus*, Lower Miocene, Patagonia. *Eurhinodelphis bossi*, Middle Miocene, Maryland.

one dorsal found in the Patagonian marine formation at Castillo, opposite Trelew, Chubut Territory, formed the basis for *Argyrocetus patagonicus* (Lydekker, 1894). This slender-beaked skull shows how widely these early Miocene porpoises have departed from the known Eocene odontocetes, for the postorbital constric- length of the premaxillaries as compared with the maxillaries, and has estimated that the former exceed the latter by an interval equivalent to one-fifth of the total length of the skull. The mandible when complete measured about 35 inches in length, of which fully three-fifths was taken up by the symphysis. Some-

thing like 50 teeth were implanted in each ramus, and ten of them were situated behind the symphysis. The latter ends in an upwardly directed and edentulous spatulate-like tip.

Further evidence that the teeth of this series of extinct porpoises were in the process of reduction is afforded by *Ziphiodelphis abeli* (Dal Piaz, 1908, 1922), whose skull and mandibles were found in the sand pits of Bolzano, Italy. Although the extremity of the rostrum is missing, this skull measures more than 30 inches in length. The anterior teeth were very much reduced in size, but the posterior maxillary teeth were functional and lodged in distinct alveoli. The alveoli disappear near the anterior end of the rostrum and merge with the alveolar groove, which indicates that the teeth near the extremity must have been held in place by a dental ligament. Unfortunately the crowns of most of the teeth are so worn that their characters are obliterated, but the few that are complete have the crowns covered with smooth enamel without basal rugosities. The mandibular symphysis is long, and the posterior angle is similar to *Eurhinodelphis*.

The lower jaws of *Eurhinodelphis bossi* (Kellogg, 1925) from the Calvert formation of Maryland are not as long as the rostrum, and the terminal portions of both jaws have no alveoli and apparently lacked teeth. In some species of this genus, as for instance *Eurhinodelphis longirostris* (Abel, 1902, 1905), the rostrum is excessively elongated, occupying nine-elevenths of the total length of the skull. Each maxilla is furnished with approximately 60 alveoli, in front of which is a narrow alveolar groove. The symphysis is slightly longer than the free portion of either mandibular ramus. Olfactory foramina are present in some species, but in others these passages are closed by the overspreading ethmoids. The nasal bones are small, and the frontals are contracted at the vertex, forming a narrow exposed strip, but sometimes are entirely covered by the supraoccipital. The lachrymal bone is either separated from the jugal by suture or ankylosed with it. The closely approximated teeth show a progressively slight increase in height and thickness posteriorly. The crowns of these teeth are slightly recurved, anteroposteriorly compressed, and covered with smooth enamel. The roots are quite variable in shape, some attentuated and others expanded distally. Judging from the number of distinct alveoli, the skull and mandibles were furnished with 220 teeth in addition to whatever number may have been present in the alveolar grooves. A reasonable estimate based on the length of the skull and the proportions of the 7 cervical, 10 or 11 dorsal, 11 lumbars, and 19 caudal vertebrae gives a total length of approximately 15 feet for this extinct porpoise. The cervical vertebrae are not ankylosed. The fore limb is similar to those of living delphinoids. The bones of this extinct porpoise are now known from Europe, North America, and Japan, in formations not later than the Upper Miocene. As to the cause of their final extinction we have no evidence other than that they had probably become so fixed and unplastic in their structure and habits that they were unable to keep pace with their associates. Toward the close of their history they become fairly numerous and seem to have been one of the dominant porpoises of the Upper Miocene.

The second series includes *Cyrtodelphis sulcatus*, a long-beaked porpoise with a very specialized and peculiar dentition, which begins its career in the Langhian stage of Europe, specimens having been

found in the coarse green quartz sands at Eggenburg, north of Vienna, Austria (Abel, 1899), in the sand pits near Belluno, Italy (Dal Piaz, 1901, 1903, and 1905), and the Uadi Faregh of Egypt (Stromer, 1905). The anterior teeth in both jaws are elongated, with pointed, lanciform, and laterally-compressed smooth-enameled crowns, the anterior and posterior edges being trenchant. These single-rooted teeth are firmly implanted in distinct alveoli, and the laterally compressed roots are abruptly expanded below the crown, forming a blade, which in some teeth is directed almost at right angles to the perpendicular axis of the crown. Posteriorly the teeth little by little diminish in height. The inwardly curved crowns become more conical with minute tubercles on inner side at base, and the roots less compressed and often thickened below the crown. The implantation of the teeth is oblique, and there were something like 50 teeth on each side in each jaw. The elongated rostrum is at least equivalent to three-fourths of the total length of the skull. The skull is further characterized by a rather flat vertex with relatively large exposure of the frontals, a small rhomboidal interparietal, and small antero-posteriorly compressed nasals; a low supraoccipital; rostrum with closely approximated premaxillaries, ankylosed together distally with age, and tapering less abruptly than the maxillaries; and olfactory foramina are present. The dorso-ventrally compressed and solidified symphysis is equivalent to two-thirds of the total length of the mandible, with a longitudinal ventral furrow on each side into which vascular foramina open. The skeleton is known to contain 7 separate cervical and 10 dorsal vertebrae.

The Lower Miocene porpoise *Cyrtodelphis* offers some points of unusual interest. Its skull was not only telescoped to a high degree, but also its complement of teeth has increased four or five fold above the normal eutherian dentition. *Cyrtodelphis* proved sufficiently adaptable to environmental conditions to leave descendants in succeeding pelagic faunas, and its several species have been found in the Helvetian stage of France, the Tortonian Calvert formation of Maryland (True, 1908), the Sarmatian of Heiligenstadt near Vienna (Abel, 1899), the Anversian of Antwerp, Belgium (Abel, 1905), and the supposedly more recent Bone Valley formation of Florida (Allen, 1921).

Another equally interesting porpoise from the Libano sand pit near Belluno has recently been described by Dal Piaz (1916) as *Eoplatanista italica*. The distinguished Italian palaeontologist considered this extinct porpoise to be a precursor of the living *Platanista* and cited the peculiarities of the teeth to support his contention. Without attempting to go into an extensive discussion of *Eoplatanista italica* and follow out each structural detail, it may be said that one can not well avoid being cognizant of the resemblance of this skull to the contemporary *Cyrtodelphis*. Similarity of structure, such as observed in these two extinct porpoises, can hardly be considered superficial. In so far as the cranium is concerned, *Eoplatanista* differs from *Cyrtodelphis* in having the vertex noticeably contracted in an antero-posterior direction and a reduced number of teeth, there being 40 teeth in each upper jaw and 38 in each lower jaw. Otherwise the contours and structural peculiarities of the skulls of these two porpoises are practically identical. The same observation holds true for the periotic bones. That the type skull of *Eoplatanista* belongs to an old individual is shown by the well worn teeth, which are ground down to or below the level of the base of the crown.

Changes in the shape of the root, such as may be observed when *Eoplatanista* is contrasted with *Cyrtodelphis*, are comparable to those in the teeth of very old individuals and mature specimens of the living *Platanista*. At any event the differences observed in the teeth are hardly of sufficient importance to warrant a family distinction between these two extinct porpoises. The skull of *Eoplatanista* measured about 26 inches in length and is thus a few inches shorter than that of *Cyrtodelphis*. Its relationships appear to be with *Cyrtodelphis*, and it is here considered to be a member of that series.

Extinct porpoises with similarly fashioned jaws, such as *Pomatodelphis* (Allen, 1921), which was characterized by a somewhat narrower symphysis, were associated with *Cyrtodelphis* in these Miocene seas.

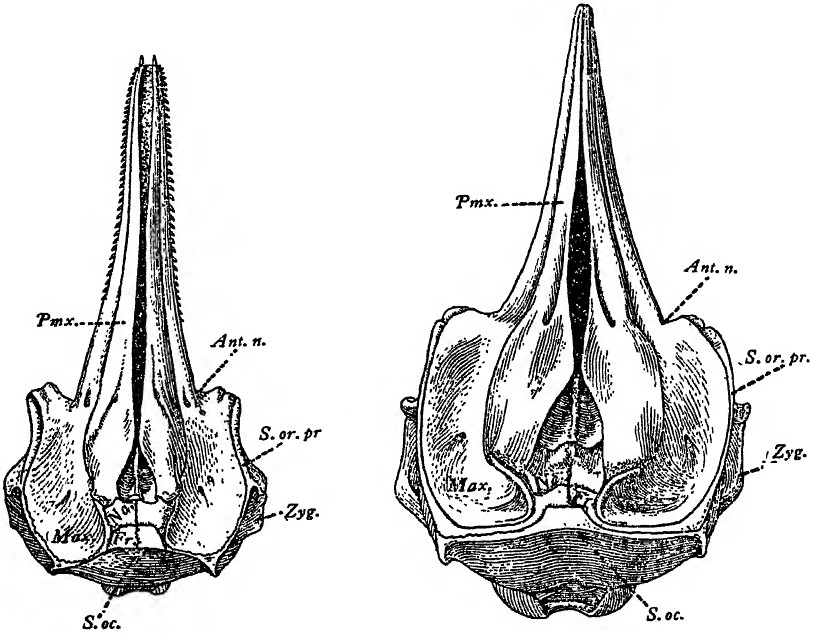
A third type of slender-beaked porpoise is that described by Abel (1899) as *Acrodelphis*, whose geologic range extends from the Langhian to the Sarmatian in Europe. As it is not the object of the present summary to give a detailed description of each species, attention will be directed to the characteristic features of this extinct porpoise. The Lower Miocene species, *Acrodelphis krahuletzi* (Abel, 1899) from the Mugel-sands of Gauderndorf, Austria, and *Acrodelphis ombonii* (Longhi, 1898) from Libano, Italy, show that this porpoise had acquired a long narrow mandibular symphysis with acute posterior angle and a large number of closely approximated single-rooted teeth. The chief point of interest in this group of somewhat smaller slender-beaked porpoises is the pseudoheterodont appearance of the teeth. The anterior teeth have a long slender crown in contrast to the shorter, blunter, and more incurved conical crowns of the posterior teeth, which are further characterized by the presence of small accessory tubercles, conspicuous basal rugosities, and a crenelated cutting edge. The stage of telescoping is similar to that of *Cyrtodelphis*, but the vertex is smaller and more convex, the frontals are restricted to a narrow strip on the vertex, and the nasal bones are relatively larger. Another closely related porpoise, *Champsodelphis*, was associated with it in the pelagic faunas of the succeeding Miocene stages. Like *Cyrtodelphis*, these extinct porpoises seem to have left no descendants in the later Tertiary.

Modernized porpoises make their appearance in increasing numbers toward the close of the Miocene epoch, and since that time there has been relatively little modification of fundamental structural details. These porpoises were followed by types that resembled their progenitors in fundamental characters but differed in more pronounced specialization of one or more structures. The Pliocene period witnessed the extinction of many aberrant and highly specialized porpoises with extremely long rostra. Mechanical difficulties apparently interfered with a further development or even a continuation of this type of rostrum. There are brevirostrine and longirostrine types among living porpoises, but none of the latter approach these Miocene types in the relative length of the rostrum.

During the time of accumulation of the Calvert formation in Maryland, several types of short-snouted porpoises, in association with some of the more highly specialized long-snouted porpoises mentioned on the preceding pages, were frequenting the estuary which covered that area. Two of these porpoises are represented in collections by nearly complete skeletons, but the others unfortunately are still imperfectly known. When one studies the skulls of these extinct

porpoises, the conclusion can not be avoided that they represent stages through which some of those now living have passed. The Calvert porpoises, *Delphinodon dividum* (True, 1912) and *Kentriodon pernix* (Kellogg, 1927), resemble some of the smaller living porpoises rather closely, and it is not unlikely that they were as active and as graceful as any of the living types.

transverse crest of the supraoccipital, extremity of rostrum formed by the premaxillaries and at least three teeth implanted in each of these bones, 40 teeth in each upper jaw and 38 in each mandible. The crowns of the teeth are recurved, with relatively smooth enamel, but with neither carinae nor accessory cusps; the roots are slender, slightly enlarged below the crown, and have a small pulp cavity.



Kentriodon pernix *Delphinodon dividum*

FIG. 10. DORSAL VIEWS OF SKULLS

Kentriodon pernix, Middle Miocene, Maryland. *Delphinodon dividum*, Middle Miocene, Maryland

There is a marked resemblance between the extinct Miocene *Kentriodon pernix* and the living southern porpoise *Sotalia tucuxi*. The skeleton of *Kentriodon* is approximately $5\frac{1}{2}$ feet long. Its telescoped skull has a short and narrow braincase, a slender rostrum, a small, more or less pentagonal vertex, the posterior extremity of the maxillary in contact with the

Sotalia on the other hand lacks the tusk-like teeth at the extremity of the jaws; no teeth are implanted in the premaxillary, for it does not project beyond the maxillary; the braincase is more expanded; and the maxillary has receded from the crest of the supraoccipital.

As compared with *Kentriodon*, the skull of *Delphinodon dividum* has a large, broad

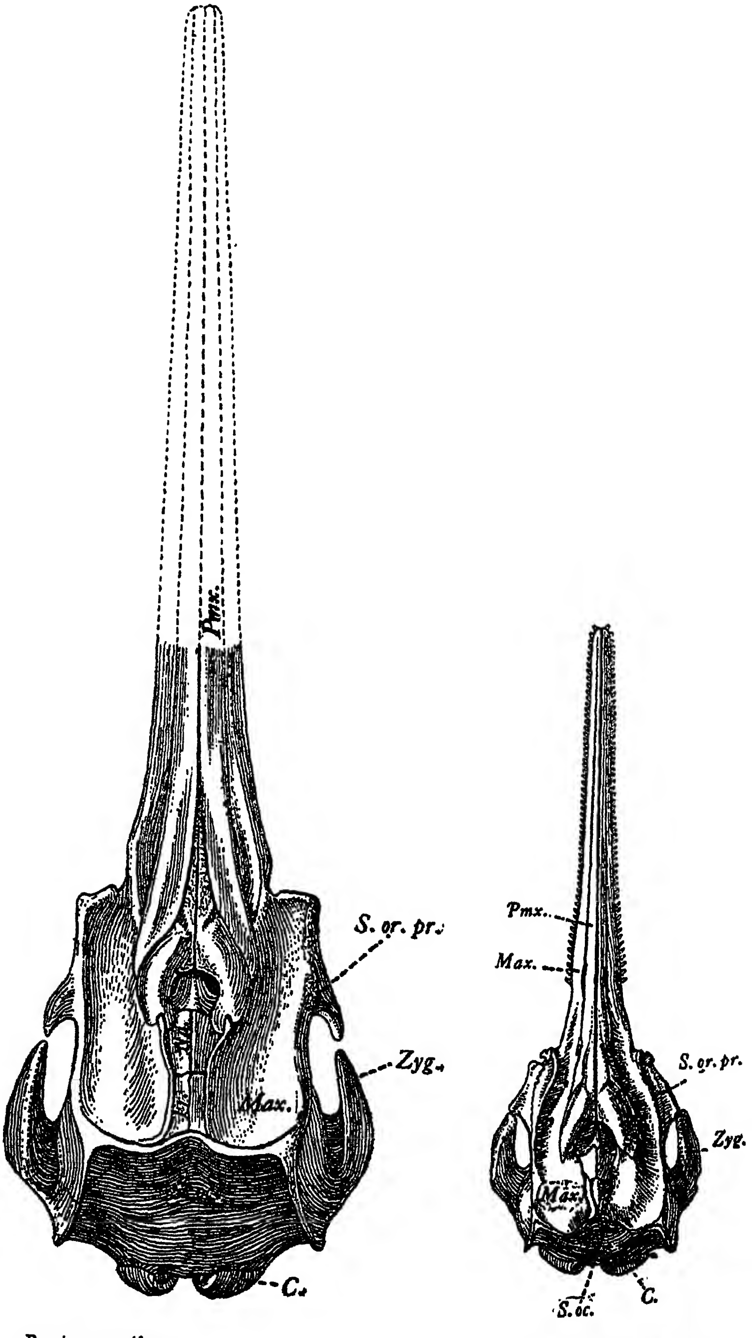
braincase, almost equal to the length of the rostrum; a strongly attentuated rostrum, whose extremity is formed by the premaxillaries, 27 teeth in each upper jaw, and 26 in each mandible. The crowns of the teeth are recurved, with rugose enamel, and distinct carinae on anterior and posterior cutting edges; posterior teeth with one or more accessory cusps; the roots are slender, gibbous below the crown, and have a large pulp cavity. The skeleton is a few inches longer than that of *Kentriodon*. The living porpoise *Cephalorhynchus* may have descended from some such type as *Delphinodon*.

There were other species of Upper Miocene porpoises whose skulls were undergoing a process of remodeling leading up to the extremely short-snouted living porpoises, such as *Neomeris*, *Phocaena*, and *Phocoenoides*. An enlargement of the braincase caused the posterior cranial elements to swell outward. Earlier porpoises have the occipital region more or less flattened in contrast to the decidedly bulging appearance of the hinder cranial region of most living delphinoids. This tendency toward enlarging the braincase resulted in further changes in the relations of certain bones. The facial region becomes broader and the tendency toward shortening and broadening the rostrum becomes more noticeable in some forms than in others. This is particularly true of the section of the delphinoids to which the living "blackfish," *Globicephala*, belongs. Porpoises with moderately long beaks are in the minority, in so far as genera are concerned, in the existing pelagic faunas.

Short-snouted porpoises, with skulls that resemble those of *Tursiops* and *Delphinapterus*, have been found at a number of localities of Pliocene age in Italy. The relations of the pterygoid and alisphenoid bones are the critical structural features that distinguish these two genera, and it is unfortunate that these details have not been ascertained. These Pliocene porpoises had not more than 66 teeth, while the living bottlenose porpoise, *Tursiops*, has a hundred or more. The trend of development in later Tertiary involves a secondary reduction of the quadrupled or quintupled dentition, and there is no evidence to indicate that recent porpoises are reversing their evolution again by undergoing an increase in the number of teeth. It is more likely that these Pliocene porpoises represent another line of development and that their descendants had the teeth further reduced. It is still uncertain whether or not the living white whale, *Delphinapterus*, which has a total of 36 teeth, is related to any of these Pliocene porpoises.

The Lower Pliocene or Plaisancian stage of Italy has at least three species of extinct porpoises that have been referred to *Tursiops*. Of these the nearly complete skeleton of *Tursiops cortesii* (Fischer, 1829; Cuvier, 1836, pl. 224, Figs. 1–2) found south of Fiorenzuola, Italy, is probably the most interesting. This has a skull with 14 teeth in each upper jaw and 14 in each mandible. Coming to the Middle Pliocene or Astian stage, we find a larger number of occurrences of extinct porpoises referred to *Tursiops*. A remarkably well preserved skull and skeleton of *Tursiops capellini* (Sacco, 1893) found near Cortazzone in the Territory of Camerano-Carasco, Italy, has 16 teeth in each upper jaw and 15 in each mandible. In both of the skeletons just mentioned the atlas and axis are fused together.

In the late Pliocene or Sicilian stage another species, *Tursiops osennae* (Simonelli, 1911) makes its appearance. This extinct porpoise has 21 teeth in the upper jaw and probably an equal number in the mandible. It was found in a



Pontistes rectifrons *Stenodelphis blainvillei*

Fig. 11. Dorsal Views of Skulls

Pontistes rectifrons, Lower Pliocene, Parana, Argentine Republic. *Stenodelphis blainvillei*, Mar de la Plata, Argentine Republic.

glauconiferous clay in the province of Siena, Italy, and seems to be a true *Tursiops*.

The living killer whale, *Orcinus orca*, seems to have descended from the same stock as *Tursiops*, and it is not unlikely that some of the confusion that exists as to the relationships of some of the Pliocene porpoises is caused by resemblances due to this common origin. In any event, an extinct killer whale *Orcinus citoniensis* (Capellini, 1883) occurs in the Middle Pliocene of Italy. A nearly complete skeleton, skull, and mandibles of this porpoise was found at Cetona in Tuscany. It has 14 teeth in each jaw, while the living killer whale has from 10 to 14.

In a similar manner, we may trace back the ancestry of the living porpoise *Steno* with a moderately long rostrum to the Middle Pliocene *Steno bellardii* (Portis, 1885) found near Asti, Italy, and the Lower Pliocene *Steno gastaldii* (Brandt, 1874) from the Piemonte district of Italy.

Slender-snouted porpoises belonging to the subfamily Stenodelphininae differ from those referred to the Delphininae by having pterygoids with large reduplications, which overspread the corresponding alisphenoid, and separate cervical vertebrae. The telescoping of the skull has proceeded along the same lines as in the Delphininae. It is fairly certain that their geological history dates back into the Miocene, and that they represent a line of descent that has paralleled the long-snouted porpoises of the Miocene. Their remains have not been recognized as yet in the Miocene formations, and it is not until the Lower Pliocene that we are aware of their presence in former pelagic faunas.

Pontistes rectifrons (Burmeister, 1885) is represented solely by a cranium, lacking the distal portion of the rostrum and the teeth, but otherwise quite complete, found in the Lower Pliocene marine deposits on the bank of the Parana River near the town of Parana, Argentine Republic. The skull shows a striking resemblance to the living *Stenodelphis*, but is twice as large in all its dimensions. It agrees with *Stenodelphis* in the squared occipital region, elevation of the premaxillaries in front of the narial passages, rather slender and somewhat pointed zygomatic processes placed far forward, and slender rostrum. The main differences as far as regards the superior aspect of the skull are that in *Stenodelphis* there is a more obvious side to side constriction of the interorbital region and the lateral margins of the maxillaries are turned upward above the orbits. Furthermore the teeth are about one-third as large and are more closely approximated. A small fragment of the rostrum of a Pleistocene porpoise recently found at San Diego, California, shows so close a resemblance to *Stenodelphis* that it tends to confirm the former existence on the Pacific Coast of a member of the subfamily Stenodelphininae. The teeth of *Stenodelphis sternbergi* (Gregory and Kellogg, 1927) have the same peculiar shape as those of *Stenodelphis*, having an axe-like root and a slender crown, but are less closely spaced. The living member of this subfamily, *Stenodelphis blainvillei*, survives in some of the fresh water streams of Argentina, Uruguay, and Brazil.

(*To be concluded*)

LIST OF LITERATURE

Abel, O. 1899. Untersuchungen über fossilen Platanistiden des Wiener Beckens. Denkschr. k. Akad. Wiss. math.-nat. Kl., Wien, vol. 68, pp. 839–874, pls. 1–4, text fig. 1.

———. 1901. Ueber die Hautbepanzerung fossiler Zahnwale. Beiträge z. Paläont. u. Geol. Österreich-Ungarns u. d. Orients, Wien, vol. 13, pt. 4, pp. 297–317, pls. 20–21, text figs. 4.

———. 1901. Les dauphins longirostres du Boldérien (Miocène supérieur) des environs d'Anvers. Part I. Mém. Mus. Roy. d'Hist. Nat. de Belgique, Bruxelles, vol. 1, pp. 1–95, pls. 1–10, text figs. 1–17.

———. 1902. Die Ursache der Asymmetrie des Zahnwalschädels. Sitzungsber. k. Akad. Wiss., Wien, vol. 111, pp. 510–526, pl. 1.

———. 1902. Les dauphins longirostres du Boldérien (Miocène supérieur) des environs d'Anvers. Part II. Mém. Mus. Roy. d. Hist. Nat. de Belgique, Bruxelles, vol. 2, pp. 101–188, pls. 11–18, text figs. 18–20.

———. 1905. Les Odontocètes du Boldérien (Miocène supérieur) d'Anvers. Mém. Mus. Roy. d'Hist. Nat. de Belgique, Bruxelles, vol. 3, pp. 1–155, text figs. 1–27.

———. 1905. Eine Stammtype der Delphiniden aus dem Miocän der Halbinsel Taman. Jahrbuche k. k. geolog. Reichsanstalt, Wien, vol. 55, pt. 2, pp. 375–388, text figs. 2.

———. 1907. Die Morphologie der Hüftbeinrudimente der Cetaceen. Denkschr. k. Akad. Wiss. math.-nat. Kl., Wien, vol. 81, pp. 139–195, text figs. 56.

———. 1909. Cetaceenstudien. II. Mittheilung: Der Schädel von *Saurodelphis argentinus* aus dem Pliozän Argentiniens. Sitzungsber. k. Akad. Wiss. math.-nat. Kl., Wien, vol. 118, pt. 1, pp. 255–272, pl. 1, text fig. 1.

———. 1912. Cetaceenstudien. III. Mittheilung: Rekonstruktion des Schädels von *Prosqualodon australe* Lyd. aus dem Miozän Patagoniens. Sitzungsber. k. Akad. Wiss. math.-nat. Kl., Wien, vol. 121, pt. 1, pp. 57–75, pls. 1–3, text fig. 1.

Allen, G. M. 1921. Fossil cetaceans from the Florida phosphate beds. Journ. Mammalogy, vol. 2, no. 3, pp. 144–159, pls. 10–12, text fig. 1.

———. 1921. A new fossil cetacean. Bull. Mus. Comp. Zool. Harvard College, vol. 65, no. 1, pp. 1–14, pl. 1, text figs. 1–3.

———. 1926. Fossil mammals from South Carolina. Bull. Mus. Comp. Zool. Harvard College, vol. 67, no. 14, pp. 447–467, pls. 1–5.

Allen, J. A. 1882. Preliminary list of works and papers relating to the mammalian orders of Cete and Sirenia. Bull. U. S. Geol. & Geogr. Surv. Terr., Washington, vol. 6, no. 3, pp. 399–598.

Ameghino, F. 1891. Caracteres diagnósticos de cincuenta especies nuevas de mammiferos fósiles argentinos. Revista Argentina de Historia Natural, Buenos Aires, vol. 1, pt. 3a, pp. 129–167, text figs. 26–75.

Andrews, C. W. 1906. A Descriptive Catalogue of the Tertiary Vertebrata of the Fayum. Publ. Brit. Mus. (Nat. Hist.), London, pp. xxxvii + 324, pls. 1–26.

———. 1920. A description of new species of zeuglodont and of leathery turtle from the Eocene of Southern Nigeria. Proc. Zool. Soc. London, no. 22, pp. 309–319, pls. 1–2, text figs. 1–3.

———. 1923. Note on the skulls from which the endocranial casts described by Dr. Dart were taken. Proc. Zool. Soc. London, no. 42, pp. 648–654, text figs. 22–24.

Andrews, Roy C. 1922. A remarkable case of external hind limbs in a humpback whale. Report Provincial Museum (British Columbia) for 1921, pp. 9–11, pls. 1–2.

Andrews, Roy C., and H. von W. Schulte. 1916. The sei whale (*Balaenoptera borealis* Lesson). Mem. Amer. Mus. Nat. Hist., New York, n.s., vol. 1, pt. 6, pp. 289–502, pls. 27–57.

Anthony, R. 1926. Les affinités des Cétacés. Ann. Inst. Océanographique (2), vol. 3, pp. 93–134, pl. 1, text figs. 25.

Bassani, F., and A. Misuri. 1912. Sopra un Delfinorinco del calcare Miocenico di Lecce (*Ziphiodelphis abeli* Dal Piaz). Mem. R. Accad. Lincei Cl. sci. fis. mat. e nat., Roma (5), vol. 9, fasc. 2, pp. 25–38, pl. 1, text figs. 1–6.

Burmeister, G. 1871. On *Saurocetes argentinus*, a new type of Zeuglodontidae. Ann. & Mag. Nat. Hist., London (4), vol. 7, pp. 51–55, pl. 1.

———. 1885. Exámen critico de los mamiferos y reptiles fósiles denominados por D. Augusto Bravard y mencionados en su obra precedente. Anales Mus. Nac. Buenos Aires, vol. 3, pp. 93–174, pls. 2–3.

———. 1891. Continuacion de las adiciones al examen critico de los mamiferos fosiles terciarios. Anales Mus. Nac. Buenos Aires, vol. 3, pp. viii + 401–461, pls. 8–10.

Cabrera, A. 1926. Cetaceos fosiles del Museo de La Plata. Revista del Museo de La Plata, Buenos Aires, vol. 29, pp. 363–411, text figs. 1–19.

CAPELLINI, G. 1883. Di un'orca fossile, scoperta a Cetona in Toscana. Mem. Accad. Sci. Ist. di Bologna (4), vol. 4, pp. 665–687, pls. 1–4.

———. 1885. Del Zifioide fossile (*Choneziphius planirostris*) scoperto nelle sabbie plioceniche di Fangonero presso Siena. Mem. R. Accad. Lincei Cl. sci. fis. mat. e nat., Roma (4), vol. 1, pp. 18–29, pl. 1, text figs. 1–10.

1887. Delfinorinco fossile dei dintorni di Sassari. Mem. Accad. Sci. Ist. di Bologna (4), vol. 8, pp. 103–110, pl. 1.

CHAPMAN, F. 1917. New or little known Victorian fossils in the National Museum. Proc. Roy. Soc. Victoria, Melbourne (n.s.), vol. 30, pt. 1, pp. 32–43, pls. 4–5.

COPE, E. D. 1890. The Cetacea. American Naturalist, Philadelphia, vol. 24, no. 283, pp. 599–616, pls. 20–23, text figs. 8.

———. 1895. Fourth contribution to the marine fauna of the Miocene period of the United States. Proc. Amer. Philos. Soc., Philadelphia, vol. 34, no. 147, pp. 135–154, pl. 6.

1896. Sixth contribution to the knowledge of the marine Miocene fauna of North America. Proc. Amer. Philos. Soc., Philadelphia, vol. 35, no. 151, pp. 139–146, pls. 11–12.

CUVIER, G. 1836. Recherches sur les Ossemens Fossiles, Paris, éd. 4, vol. 8, pp. 153–321; Atlas, vol. 2.

DAL PIAZ, G. 1901. Di alcuni resti di *Cyrtodelphis sulcatus* dell'arenaria miocenica di Belluno. Palaeontographia Italica, Pisa, vol. 7, pp. 287–292, pl. 34.

———. 1903. Sugli avanzi di *Cyrtodelphis sulcatus* dell'arenaria di Belluno. Part I. Palaeontographia Italica, Pisa, vol. 9, pp. 187–220, pls. 28–31, text figs. 16.

———. 1904. *Neosqualodon* nuovo genere della famiglia degli Squalodontidi. Mém. Soc. Paleont. Suisse, Genève, vol. 31, no. 5, pp. 1–19, pl. 1.

———. 1905. Sugli avanzi di *Cyrtodelphis sulcatus* dell'arenaria di Belluno. Pt. II. Palaeontographia Italica, Pisa, vol. 11, pp. 253–280, pls. 18–21, text figs. 17–26.

———. 1908. Sui vertebrati delle arenarie Mioceniche di Belluno. Atti Accad. sci. veneto-trentino-istriana, Padova, Cl. I, Anno V, pp. 1–19, text figs. 7.

———. 1916. Gli Odontoceti del Miocene Bellunese. Part II. *Squalodon*. Mem. Ist. Geol. R. Univ. di Padova, vol. 4, pp. 1–94, pls. 11, text figs. 1–10.

———. 1916. Gli Odontoceti del Miocene Bellunese. Part III. *Squalodelphis fabianii*. Mem. Ist. Geol. R. Univ. di Padova, vol. 5, pp. 1–34, pls. 1–5.

DAL PIAZ, G. 1916. Gli Odontoceti del Miocene Bellunese. Part IV. *Eoplatanista italica*. Mem. Ist. Geol. R. Univ. di Padova, vol. 5, pp. 1–23, pls. 1–2.

———. 1922. L'Istituto geologico dell'Università di Padova nel 1922. Notizie Sommarie. Mem. Ist. Geol. R. Univ. di Padova, vol. 6, pp. 1–15, text figs. 1–8.

DAMES, W. 1894. Über Zeuglodonten aus Ägypten und die Beziehungen der Archaeoceten zu den übrigen Cetaceen. Geol. u. Palaeont. Abhandl., Jena, N.F., vol. 1, pp. 189–222, pls. 30–36, text fig. 1.

DEINSE, A. B. VAN. 1927. On fossil Cetacea and Pinnipedia in the Netherlands. Proc. K. Akad. Wetenschappen, Amsterdam, vol. 29, no. 10, pp. 1356–1364.

DEL PRATO, A. 1897. Il *Tursiops Capellini* Sacco del Pliocene Piacentino. Palaeontographia Italica, Pisa, vol. 3, pp. 1–14, pl. 1.

EASTMAN, C. R. 1907. Types of fossil cetaceans in the museum of Comparative Zoology. Bull. Mus. Comp. Zool. Harvard College, vol. 51, no. 3, pp. 79–94, pls. 1–4, text figs. 2.

FEDOROWSKIJ, A. 1912. Zeuglodon-Reste aus dem Kreise Zmijew Gouvernement Charkow. Charikov. Trav. Soc. Nat., vol. 45, pp. 253–287, pls. 1–3, text figs. 6.

FISCHER, J. B. 1829. Synopsis Mammalium. Stuttgart, pp. xlii + 527.

FLOT, L. 1896. Note sur les Cétacés fossiles de l'Aquitaine. Bull. Soc. Géol. de France, Paris (3), vol. 24, pp. 270–282, pls. 7–8, text figs. 1–9.

FLOWER, W. H. 1868. On the osteology of the cachalot or sperm whale (*Physeter macrocephalus*). Trans. Zool. Soc. London, vol. 6, pt. 6, pp. 309–372, pls. 55–61, text figs. 1–13.

———. 1883. On whales, past and present, and their probable origin. Proc. Roy. Instit. Great Britain, London, vol. 10, pp. 360–376.

FORBES, H. O. 1893. Observations on the development of the rostrum in the cetacean genus *Mesoplodon*, with remarks on some of the species. Proc. Zool. Soc. London, pp. 216–236, pls. 12–15, text figs. 2.

FRAAS, E. 1904. Neue Zeuglodonten aus dem unteren Mitteleocän vom Mokattam bei Kairo. Geol. u. Palaeont. Abhandl., Jena, vol. 10, pt. 3, pp. 199–220, pls. 10–12.

FRENGUELLI, J. 1922. *Prionodelphis rovereti* un representante de la familia "Squalodontidae" en el Paranense superior de Entre Rios. Bol. Acad. Nac. Ciencias en Córdoba (República Argentina), vol. 25, pp. 491–500, text figs. 1–2.

GEMMELLARO, M. 1921. Il *Neosqualodon assenzae*, Forsyth Major sp. del Museo Geologico della

Università di Palermo. Giornale Sci. Nat. ed Econ. di Palermo, vol. 32, pt. 2, pp. 121–154, pl. 1, text figs. 4.

Gervais, P. 1848–1852. Zoologie et Paléontologie Françaises, Paris, vol. 1, pp. viii + 271; vol. 2, pp. 142; vol. 3, atlas, pls. 80.

———. 1861. Sur différentes espèces de vertébrés fossiles observées pour la plupart dans la Midi de la France. Mém. Acad. Sci. et Let. de Montpellier, vol. 5, pt. 1, pp. 117–132, pl. 4.

1871. Remarques sur l'anatomie des Cétacés de la division des Balénidés tirées de l'examen des pièces relatives à ces animaux qui sont conservées au Muséum. Nouv. Archiv. Mus. Hist. Nat., Paris, vol. 7, fasc. 2, pp. 65–146, pls. 3–10.

Gidley, J. W. 1913. A recently mounted Zeuglodon skeleton in the United States National Museum. Proc. U. S. Nat. Mus., vol. 44, publ. 1975, pp. 649–654, pls. 81–82, text figs. 3.

Gray, J. E. 1866. Catalogue of seals and whales in the British Museum. Publ. Brit. Mus. (Nat. Hist.), London, ed. 2, pp. vii + 402, text figs. 101.

Gregory, W. K., and R. Kellogg. 1927. A fossil porpoise from California. Amer. Mus. Novitates, No. 269, pp. 1–7, text figs. 3.

Guldberg, G., and F. Nansen. 1894. On the development and structure of the whale. Part I. On the development of the dolphin. Bergens Museum, Bergen, pp. 1–70, pls. 1–7.

Hall, T. S. 1911. On the systematic position of the species of *Squalodon* and *Zeuglodon* described from Australia and New Zealand. Proc. Roy. Soc. Victoria, Melbourne, (n.s.), vol. 23, pt. 2, pp. 257–265, pl. 36.

Harlan, R. 1834. Notice of fossil bones found in the Tertiary formation of the State of Louisiana. Trans. Amer. Philos. Soc., vol. 4, pp. 397–403, pl. 20, text figs. 1–2.

Harmer, S. F. 1924. On *Mesoplodon* and other beaked whales. Proc. Zool. Soc. London, pt. 2, pp. 541–587, pls. 1–4, text figs. 3.

———. 1927. Report on Cetacea stranded on the British Coasts from 1913 to 1926. Publ. 10, Brit. Mus. (Nat. Hist.), London, pp. 91, text figs. 42, maps 7.

Hunter, J. 1787. Observations on the structure and oeconomy of whales. Philos. Trans. Roy. Soc. London, vol. 77, pt. 2, pp. 371–450, pls. 16–23.

Japha, A. 1910. Die Haare der Waltiere. Zool. Jahrb., Abth. f. Anat., pp. 1–43, pls. 1–3.

Jardine, W. 1837. The Naturalist's Library. Mammalia, vol. 6. On the ordinary Cetacea or Whales. Edinburgh, pp. 264, pls. 29.

Kellogg, R. 1923. Description of two squalodonts recently discovered in the Calvert cliffs, Maryland; and notes on the shark-toothed cetaceans. Proc. U. S. Nat. Mus., vol. 62, publ. 2462, pp. 1–69, pls. 1–20.

———. 1923. Description of an apparently new toothed cetacean from South Carolina. Smithsonian Misc. Coll., vol. 76, publ. 2723, pp. 1–7, pls. 1–2.

———. 1925. On the occurrence of remains of fossil porpoises of the genus *Eurhinodelphis* in North America. Proc. U. S. Nat. Mus., vol. 66, publ. 2563, pp. 1–40, pls. 1–17, text figs. 1–4.

———. 1927. *Kentriodon pernix*, a Miocene porpoise from Maryland. Proc. U. S. Nat. Mus., vol. 69, publ. 2645, pp. 1–55, pls. 1–14, text figs. 1–20.

Gorjanović-Kramberger, D. 1892. O Fosilnih Cetaceih Hrvatske i Kranjske. Rad jugoslavenske akad. znanosti i umjetnosti, Zagreb, vol. 111, pp. 1–21, pls. 1–3.

Kükenthal, W. 1893. Vergleichend-anatomische und entwicklungsgeschichtliche Untersuchungen an Walthieren. Denkschr. med.-naturwiss. Gesell., Jena, vol. 3, pp. 224–338, pls. 14–25, text figs. 115.

———. 1922. Zur Stammesgeschichte der Wale. Sitzungsb. preuss. Akad. Wiss. Phys.-math. Kl., Berlin, pp. 72–87.

Leidy, J. 1869. The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. Journ. Acad. Nat. Sci. Philadelphia (2), vol. 7, pp. 1–472, pls. 30.

———. 1877. Description of vertebrate remains, chiefly from the phosphate beds of South Carolina. Journ. Acad. Nat. Sci. Philadelphia (2), vol. 8, pt. 3, pp. 209–261, pls. 30–34.

Longhi, P. 1898. Sopra i resti di un cranio di *Campsodelphis* fossile scoperto nella molassa miocenica della Bellunese. Atti Soc. Veneto-Trentino Sci. Nat., Padova (2), vol. 3, fasc. 2, pp. 323–381, pls. 1–3.

Lonnberg, E. 1923. Cetological notes. Arkiv för Zoologi utgivet av K. Svenska Vetenskapsakademien, Stockholm, vol. 15, no. 24, pp. 1–18, text figs. 1–6.

Lortet, L. 1887. Note sur le *Rhizoprion bariensis* Jourdan. Archiv. Mus. d'hist. nat. Lyon, vol. 4, pp. 315–316, pls. 25bis-25ter.

Lull, R. S. 1914. Fossil dolphin from California. Amer. Journ. Sci. (4), vol. 37, pp. 209–220, pl. 8, text figs. 1–7.

Lydekker, R. 1894. Contributions to a knowledge of the fossil vertebrates of Argentina. Part II. Cetacean skulls from Patagonia. Annales del

Museo de La Plata, vol. 2 for 1893, pp. 1–14, pls. 1–6, text figs. 2.

Matsumoto, H. 1926. On some fossil cetaceans of Japan. Science Reports Tôhoku Imp. Univ. Geology], Sendai, (2), vol. 10, no. 1, pp. 17–27, pls. 8–10, text figs. 5.

Miller, G. S. Jr. 1923. The telescoping of the cetacean skull. Smithsonian Misc. Coll., vol. 76, publ. 2720, pp. 1–70, pls. 8.

Moreno, F. P. 1892. Lijeros apuntes sobre dos géneros de Cetáceos fósiles de la República Argentina. Revista del Museo de La Plata, vol. 3, pp. 393–400, pls. 10–11.

Müller, J. 1849. Über die fossilen Reste der Zeuglodonten von Nordamerica mit Rücksicht auf die europäischen Reste aus dieser Familie. Berlin, pp. iv + 38, pls. 1–27.

Oliver, W. R. B. 1922. A review of the Cetacea of the New Zealand seas. Proc. Zool. Soc. London, pp. 557–585, pls. 1–4.

Owen, R. 1839. Observations on the *Basilosaurus* of Dr. Harlan (*Zeuglodon cetoides* Owen). Trans. Geol. Soc. London (2), vol. 6, pp. 69–79, pls. 7–9.

———. 1870. Monograph on the British fossil Cetacea from the Red Crag. No. 1, Containing Genus *Ziphius*. Palaeontographical Society for 1869, London, pp. 1–40, pls. 1–5, text figs. 1–14.

Papp, C. V. 1905. *Heterodelphis leiodontus* nova forma aus den Miocenen Schichten des Comitates Sopron in Ungarn. Mitteil. Jahrb. Kgl. Ungarischen Geol. Anstalt, Budapest, vol. 14, pt. 2, pp. 23–61, pls. 1–2, text figs. 1–10.

Paquier, V. 1894. Étude sur quelques Cétacés du Miocène. Mém. Soc. Geol. France, Paléont., Paris, vol. 4, fasc. 4, pp. 1–20, pls. 17–18.

Portis, A. 1885. Catalogo descrittivo dei Talassoterii rinvenuti nei Terreni Terziarii del Piemonte e della Liguria. Mem. R. Accad. Sci. Torino (2), vol. 37, pp. 247–365, pls. 1–9.

———. 1925. Resti di Cetacei (Odontoceti, Delphinoceti) dal Pliocene argilloso delle vicinanze di Roma. Boll. R. Ufficio geol. d'Italia, Roma, vol. 50, no. 3, pp. 1–19.

Ray, J. 1671. An account of the dissection of a porpess. Philos. Trans. Roy. Soc. London, vol. 6, no. 76, pp. 2274–2279.

Rovereto, C. 1915. Nuevas investigaciones sobre los Delfines Longirrostros del Mioceno del Paraná (República Argentina). Ann. Mus. Nac. Buenos Aires, vol. 28, pp. 139–151, pls. 2–4.

Sacco, F. 1893. Il Delfino pliocenico di Camerano Casasco (Astigiana). Mem. Soc. Italiana Sci., Napoli (3a), vol. 9, no. 5, pp. 1–14, pls. 1–2.

Simonelli, V. 1911. Avanzi di "*Tursiops*" del Pliocene Senese. Mem. R. Accad. Sci. Ist. di Bologna (6), vol. 8, pp. 249–260, pl. 1, figs. 1–14.

Stromer, E. 1903. Zeuglodon-Reste aus dem oberen Mitteleocän des Fajûm. Beiträge z. Paläont. u. Geol. Österreich-Ungarns u. d. Orients, Wien, vol. 15, pts. 2–3, pp. 65–100, pls. 8–11, text fig. 1.

———. 1905. Fossile Wirbeltier-Reste aus dem Uadi Fâregh und Uadi Natrûn in Ägypten. Abhandl. Senckenberg. naturf. Ges., Frankfurt a.M., vol. 29, pt. 2, pp. 99–132, pl. 20, text fig. 1.

———. 1908. Die Archaeoceti des Ägyptischen Eozäns. Beiträge z. Paläont. u. Geol. Österreich-Ungarns u. d. Orients, Wien, vol. 21, pp. 106–177, pls. 4–7.

True, F. W. 1889. Contributions to the natural history of the cetaceans, a review of the family Delphinidae. Bull. No. 36, U. S. Nat. Mus., pp. 1–191, pls. 1–47.

———. 1907. Remarks on the type of the fossil cetacean *Agorophius pygmaeus* (Müller). Special Publ. 1694, Smithsonian Institution, pp. 1–8, pl. 1.

———. 1907. Observations on the type specimen of the fossil cetacean *Anoplonassa forcipata* Cope. Bull. Mus. Comp. Zool. Harvard College, vol. 51, no. 4, pp. 97–106, pls. 1–3.

———. 1908. On the occurrence of remains of fossil cetaceans of the genus *Schizodelphis* in the United States, and on *Priscodelphinus* (?) *crassangulum* Case. Smithsonian Misc. Coll., vol. 50, publ. 1782, pp. 449–460, pls. 59–60.

———. 1908. The fossil cetacean, *Dorudon serratus* Gibbes. Bull. Mus. Comp. Zool. Harvard College, vol. 52, no. 4, pp. 65–78, pls. 1–3.

———. 1909. A new genus of fossil cetaceans from Santa Cruz Territory, Patagonia; and description of a mandible and vertebrae of *Prosqualodon*. Smithsonian Misc. Coll., vol. 52, publ. 1875, pp. 441–456, pls. 43–45.

———. 1910. Description of a skull and some vertebrae of the fossil cetacean *Diochotichus vanbenedeni* from Santa Cruz, Patagonia. Bull. Amer. Mus. Nat. Hist., vol. 28, pp. 19–32, pls. 1–5.

———. 1910. An account of the beaked whales of the family Ziphiidae in the collection of the United States National Museum, with remarks on some specimens in other American Museums. Bull. No. 73, U. S. Nat. Mus., pp. 1–89, pls. 1–42.

———. 1912. A fossil toothed cetacean from California, representing a new genus and species.

Smithsonian Misc. Coll., vol. 60, publ. 2151, pp. 1–7, pls. 1–2.

True, F. W. 1912. Description of a new fossil porpoise of the genus *Delphinodon* from the Miocene formation of Maryland. Journ. Acad. Nat. Sci. Philadelphia (2), vol. 15, pp. 163–194, pls. 17–26.

Van Beneden, P. J. 1865. Recherches sur les ossements provenant du Crag d'Anvers, Les Squalodons. Mém. Acad. Roy. Sci. Belgique, Bruxelles, vol. 35, pp. 1–85, pls. 1–4.

———. 1868. Recherches sur les Squalodons. Supplément. Mém. Acad. Roy. Sci. Belgique, Bruxelles, vol. 37, pp. 1–13, pl. 1, text figs. 2.

———. 1869. Sur un nouveau genre de Ziphiöide Fossile (*Placoziphius*), trouvé à Edeghem, près d'Anvers. Mém. Acad. Roy. Sci. Belgique, Bruxelles, vol. 37, pp. 1–13, pls. 1–2.

———. 1883. Sur quelques ossements de Cétacés fossiles recueillis daus couches phosphatées entre l'Elbe et le Weser. Bull. Acad. Roy. Sci. Belgique, Bruxelles (3), vol. 6, no. 7, pp. 27–33.

Van Beneden, P. J. and P. Gervais. 1880. Ostéographie des Cétacés vivants et fossiles. Paris, Text, pp. 1–605; Atlas, folio pls. 1–64.

Vigliarolo, G. 1894. Dei generi *Micropteron, Dioplodon* e *Rhinostodes* e di una nuova specie fossile di *Rhinostodes* scoperta nel calcare elveziano di Cagliari. Atti R. Accad. Sci. fis. e mat., Napoli (2), vol. 6, no. 5, pp. 1–40, pls. 1–2.

Weber, M. 1887. Ueber die cetoide Natur der Promammalia. Anat. Anz., vol. 2, pp. 42–55.

———. 1917. Über *Choneziphius planirostris* (G. Cuv.) aus der Westerschelde. Sammlungen Geol. Reichs-Mus. Leiden, N. F., vol. 2, pt. 8, pp. 309–313, pl. 1.

Winge, H. 1921. A review of the interrelationships of the Cetacea. Smithsonian Misc. Coll., vol. 72, publ. 2650, pp. 1–97. [Translation by G. S. Miller, Jr., of Winge, H. 1918. Udsigt over Hvalernes indbyrdes Slaegtskab. Vidensk. Medd. fra Dansk. naturh. Foren., vol. 70, pp. 59–142.]

Zittel, C. A. 1877. Ueber *Squalodon bariensis* aus Niederbayern. Bericht Naturh. Vereins Augsburg, vol. 24, pp. 19–46, pl. 1.

RECENT DEVELOPMENTS IN THE PHILOSOPHY OF BIOLOGY

By JOSEPH NEEDHAM

Gonville and Caius College, University of Cambridge

INTRODUCTION

The immutability of philosophical thought meets the changefulness of the science of biology in that difficult region, which is yet so attractive, the abstract aspects of the study of living things. The philosophy of biology, as it is usually called, is a most unsatisfactory name, for it implies that the philosopher may be defined as the reverse of the specialist who knows continually more and more about less and less. But philosophy is to be understood here in a much wider sense than metaphysics, and must be thought of as part of the theory of scientific investigation as a whole, the self-criticism of the scientific method, and the fascinating attempt to prophesy before the event whether indeed all the realm of living phenomena will follow the inorganic world into the obedience of mathematics. Nobody doubts that Laplace's calculator could have known all about the geology of our era, but whether he could have predicted the constitution and behavior of our standard white rats, and what they think of our feeding experiments, is another matter, and a point of faith on which many a biologist would prefer to be silent.

Reassessments in philosophy are only needed once or twice in a century, though in biology special journals called Reviews have to be provided entirely for them. Progress in the theory of biology stands midway between these extremes. Unlike philosophy proper, the theory of biology is by no means independent of experimental results, although it is true that it needs a very well-aimed stone to trouble her remoter waters. But as will be seen in the reassessment that I propose to make in this paper, now and then experimental results do appear that exercise a very definite influence on the development of the philosophy of biology. Indeed, in the last resort, since we deal here with matters that are more scientific than metaphysical, the final appeal will be to the facts and not to reason, for the biologist like any other scientific worker must be an empiricist to the end.

THE CONCEPT OF THE ORGANISM

The theoretical standpoint that can best be called "Organicism" is probably the most important factor in these considerations at the present time. The word was originally coined by Delage (11) for his great work on biological theory and was used by him in connection with the ideas of Bichat, von Baer and Roux. It was, however, given an entirely new lease of life in 1917 by J. S. Haldane (19), who then used it to describe his own views. These are so familiar to biologists that there cannot be any necessity to repeat them here; it will suffice to say that for him the

living organism as a whole with all its complicated phenomena of regulation presented features that it was impossible to imagine in any constellation of purely physico-chemical processes. The tendency of the organism to maintain its external and internal environments absolutely constant at its own optimum, the *vis medicatrix naturae*, and the preservation of individuality in living organisms, all were adduced by him as examples of phenomena so different from those of the inanimate world that conceptions quite foreign to physics and chemistry would be necessary to account for them in a reasonable manner. Moreover, he felt strongly that these conceptions were in a sense more profound than those of mechanics, and in 1919 he thought it right to maintain that far from physiology being reducible to physics and chemistry, the latter might be reducible to the former. "That a meeting-place," he said (20) "between biology and physical science may at some time be found, there is no reason for doubting. But we may confidently predict that if this meeting place be found, and one of the two sciences is swallowed up, it will not be biology."

This theme, like so many others in these regions was not quite new and had had some interesting historical relationships. Cagniard de Latour and others, for instance, had difficulty in persuading biochemists of the necessity of the yeast-cell in fermentation, owing to their distaste for attributing chemical processes to "vital activity." As a prophecy it has borne fruit very much more rapidly than that famous one of Kant's about the blade of grass, though as in that case we still cannot be sure whether the true messiah has arrived or no. Fulfilment of Haldane's prophecy may perhaps be seen in the fundamental work of A. N. Whitehead, who in his book *Science and the Modern World* (56), sets out an organic theory of nature. Still more recently a most lucid commentary and amplification of his suggestions has been given by C. Lloyd Morgan (39). The concept of the organism is now carried over into the inorganic world, and the whole universe is regarded as being made up of organisms, some of greater complexity than others but all possessing the properties of organisms. The distinguishing feature of an organism is that its parts are not entities having a full existence by themselves, but rather owe their being to the whole of which they form parts—so that if the whole is taken to pieces, the parts entirely cease to be what they were. Each part is what it is not in its own peculiar right, but by virtue of its relatedness to all the other parts in the whole. Already in *Life, Mind, and Spirit* (38), Lloyd Morgan had maintained that this kind of relatedness of parts within wholes was not a criterion of living things sufficient to distinguish them from non-living things, and A. N. Whitehead has worked out in great detail the concept of the organism in the physico-chemical world. To say that there is the same kind of internal inter-relatedness about physico-chemical organisms as about living organisms or social organisms is not to assert that there is no difference between these sorts of organism. The most extreme of the old-fashioned biological materialists never denied that there were differences between living animals and inorganic systems, for that would have been too obviously contrary to common sense; he simply said that the differences were of degree and not of kind, that the former, in a word, were only complicated special cases of the latter, whereas his opponents definitely brought in something new.

It is this in the modern extension of the concept of the organism that is so impor-

tant for the theory of biology. It means—if recent "organicism" is justified and maintains the positions it has gained—that another middle line of partition between living matter and dead matter is to be abandoned. There have been many of them, but none have withstood the advance of exact biology. If this process is followed historically it can be seen how the two most obstinate and irreducible characteristics of life were its finalistic or teleological aspects and its special arrangement in organisms, entities with a high degree of internal relatedness and dependence. The former of these has vanished with the realization of the teleology of the inorganic world, an event that will always be associated with the name of Lawrence Henderson, and now the latter would appear also to be universally present throughout nature. "Some biologists" says Lloyd Morgan (39) "interpret all organic action in the modal terms appropriate to physics and chemistry, others there are whose interpretation is couched in the modal terms appropriate to psychology. It is difficult to see on what logical grounds biologists of the first school—the so-called mechanists—can resent the downward extension of the connotation of the word 'organism' to natural entities which as they claim differ only in their lack of superadded complexity and no wise essentially in type of action or behavior. It is, however, easy to see on what logical grounds biologists of the other school—the so-called vitalists—can resent, and will no doubt reject, a concept of the organism which implies that it can adequately be discussed in terms of an organic theory of nature without introducing any further concept such as entelechy or élan." I suggest that the discovery of the value of the concept of the organism in the philosophical aspection of physico-chemical phenomena, is of great importance for the theory of biology. Workers in exact biology would in any case have had to go on using mechanism as a working principle in research, because as is well known it is the only one that will work; but it will relieve them to learn that the concept of the organism is no longer purely biological. The field of physics and chemistry, which was formerly covered by the mechanistic schema, continues to be so covered, only now the concept of the organism covers it also. Whereas until recent times, mechanism was held to be the only way of interpreting physico-chemical phenomena, while there was great doubt as to whether mechanism or organicism was the only way of interpreting life phenomena, now both mechanism and organicism come into force over both domains of experience. In other words we have to deal not with two opposing and incompatible modes of explanation struggling between themselves for fragments of our experience, but rather with two complementary and different modes of explanation covering the entire expanse of living and non-living things. If we reserve the name of science for the mechanistic mode of interpretation we shall only be obeying a necessary outcome of the quantitative and metrical character of the scientific method, and organicism, covering both realms as it now claims to do, we shall term a philosophical theory. Thus to the scientific mind the living and the non-living form one continuous series of systems of differing degrees of complexity, all of which consist of parts that can be understood as parts when separated from their wholes and are therefore interpretable in terms of "metrical macroscopic mechanism;" while to the philosophic mind the whole universe, itself perhaps an organism, is composed of a vast number

of interlacing organisms of all sizes. Organisms explode into nothing when taken to pieces, systems remain in the form of parts the relations of which can be understood. In this way the incurably analytic character of science contributes its force to the conclusion that anything may be subjected to scientific study but nothing sucked entirely dry of significance by so doing.

Thus if J. S. Haldane's prophecy has been fulfilled, it is not without a certain irony. Physics has not swallowed up physiology nor on the other hand has physiology swallowed up physics; they have devoured each other and of the old antithesis nothing is left.

To what extent the relegation of the concept of the organism to philosophy is absolute must still, however, be considered a little uncertain. In spite of its history as measured in years, the concept is still so young that we are not yet sure whether there is a sense in which the term would be applicable to a scientific hypothesis pure and simple. It is just conceivable that organicism might stand in the peculiar position of being a scientific hypothesis as well as a philosophical theory. The most important factor in this situation is the work of C. D. Murray (40, 41). In several recent papers this physiologist has applied the principle of minimum work to physiological organisms, and his success has already been very considerable. In Murray's view, the concept of organization is definitely not an "affair of the reflective judgment" but a very legitimate field for scientific experiment and calculation. Murray considers that at least two statistical laws may be obtained from the study of living organisms, both of which afford a quantitative expression of the complex systems in question. The first of these he terms the "principle of maintenance of steady states"—this would correspond to the maintenance of constancy of external and internal environment—and the second, the "principle of minimum work." This second principle states that the cost of operation of physiological systems tends always to be a minimum, and thus is an extension of the well-known principle of Lagrange. Murray works out this conception in its relations to the physiology of the circulation and gives a preliminary answer, at any rate, to the question, "In any extra effort by the organism as a whole, how is the tax or effort distributed among the various organs of the body (the parts of the whole) and what does each contribute to the extra effort of the whole?" This is certainly a most important section of the problem of organization. The principle of minimum work has the great value of defining mathematically the distribution of function among the parts of the organism. But the undecided question is, whether the word organism means here the same thing as it does in Whitehead and Lloyd Morgan. It is very doubtful whether it does, for an organism in their language means a whole that does not exist dismembered in the constituent parts, and can only be understood as a whole. There would appear to be three ways at least of thinking about a bicycle, (a) to regard it as an object capable of movement and only truly seen in its wholeness (Whitehead and Lloyd Morgan), (b) to analyze it in the confidence that the relation between the parts can be understood in isolation and systematically 1. without actually taking it to pieces (Murray) and 2. with actual analysis (the majority of biophysicists and biochemists). In any case, the slight residuum of organicism left behind in science by the transplantation of the concept of the organism into a general philosophical theory of nature will no doubt be readily

dealt with by the scientific method. Summed up as it is in Wordsworth's "We murder to dissect" organicism is certainly far from characteristic of the scientific mind.

LIVING MATTER AND THERMODYNAMICS

The relations of living systems to the law of entropy have been considered again and again during the last fifty years, and now very recently the question has been reopened by F. G. Donnan. That living things should be in some way exempt from the otherwise universal law that free energy tends always to decrease in amount in the known universe and entropy to increase, has many times been asserted, though without any evidence. The earliest hint of this is found in the writings of Lord Kelvin, then Sir. W. Thomson, who said as long ago as 1852 "It is impossible by means of *inanimate* material agency to derive mechanical effect from any portion of matter by cooling it below the temperature of the coldest of surrounding objects" (52). Thus, as Guye says, Thomson was already making reservations on the applicability of Carnot's principle to the mechanism of living systems. Then in 1882 H. von Helmholtz (24) definitely suggested that living cells might have some way of eluding Carnot's principle. In a paper read before the Berlin Academy of Sciences on February 2 of that year he said in a footnote, referring to the impossibility of any increase of free energy: "Whether such a change would also be impossible in the fine structure of living organized tissue appears to me still to be an open question, the importance of which in the economy of nature is very obvious."

Here there was already the hint of the mechanism by means of which this might be done. The appreciation of the statistical nature of the second law, gave it, however, much greater precision. James Johnstone (29) and G. N. Lewis (31) more recently both decided that living things and living things alone can retard the accumulation of entropy. Now obviously the most astonishing things may be hidden by statistical treatment. Somewhere in the universe water may run uphill, though as a whole, and in general, it does not do so. The treatment of men on a statistical basis furnishes results of great value, but there we know directly and by observation how individual the individual is. This may be also the case with molecules, and it is a commonplace that to an intelligence such as a Clerk-Maxwell demon they may have very pronounced individuality. As G. N. Lewis says, there is certain astronomical evidence that indicates the existence of disentropic phases in the universe, phases in which the amount of bound energy is diminishing instead of increasing; it is, therefore, equally possible that in the living body there are also phases where the statistical second law does not truly apply. That living plants retard the accumulation of entropy by storing free energy is undeniable, but that any living system ever reverses this process is another matter. Nevertheless both Johnstone and Lewis regard it as the main characteristic of life, as does Driesch (13), who says "Es gibt seine Dämonen. Wir selbst sind sie!"

In 1919 Guye (17) devoted some space to the examination of this question. He showed clearly that the high efficiency of physiological systems in no way proved that they functioned contrary to Carnot's principle, but rather that they were not true heat engines, a fact quite well appreciated by physiologists. He also demonstrated that the retardation of entropy-increase by the green plant was a process that could be paralleled in several non-living systems, for instance, the evaporation of the oceans.

But the realization of the statistical nature of the Carnot principle had certain implications for biological theory. If the law of entropy may justly be compared to the law that a large and equal number of black and white grains shaken up will produce a grey powder, then two considerations emerge. Firstly, the sorting out of the grains could be accomplished by a Maxwell demon—in Lewis' terminology, a cheat—acting in the system, and secondly, by prolonging the agitation till a fluctuation of a very rare type led back to the original condition, on the basis of Heraclitus' remark—"If one is sufficiently lavish with time, everything possible happens"—surely not due to Herodotus as Guye would attribute it. This reminds one of F. R. Japp's refusal (27) to believe that if a font of type was shaken up in a bag, the text of Hamlet could possibly result, however long this was continued, and of P. F. Frankland's reply (14) that if the time allowed was infinite, Hamlet must result. What is sure, at any rate, is that the statistical nature of Carnot's principle does not preclude such a rare fluctuation, nor less rare minor ones tending in the same direction. As Johnstone said, a philosophical consideration of this subject must take into account chances which even an insurance company would at once set aside as of no matter. Now "The fluctuations," says Guye (18), "which can occur in a given element of volume are in general the more important the smaller the number of molecules contained in the homogeneous element of volume considered. The reply to the foregoing question will depend therefore, on the degree of tenuity which is attributed to the structure of the tissues and of the living matter."

This is, indeed the aspect of the question that has recently been engaging attention. A. V. Hill (25) came to the conclusion recently that "It is conceivable that the ultimate minute mechanism especially of the smallest living cells, may somehow be able to evade the statistical rules which govern larger systems; it may for example like Maxwell's demon be able to sort molecules, to use the energy of the more rapidly-moving, to employ a unidirectional permeability, and so to avoid the general increase of entropy which appears to be the governing factor in all other material change. Such an evasion, if established, would be of ultimate philosophical, biological, and practical importance; there is no evidence, however, of any value, that it really occurs." F. G. Donnan (12), on the other hand, has recently made some calculations which if they do no more, at least keep open the possibility; he has attempted to estimate the size of the element of volume within which an evasion of the second law would be likely to take place. He shows how for all ordinary cases the probable fluctuations from the equilibrium state would be quite imperceptible, in other words, the chances would be immeasurably against any deviation from Carnot's principle. But for a small cubical particle of side 0.1μ consisting wholly of molecules of molecular weight 10,000 the relative thermodynamic probability of an easily detectable fluctuation from the chemical equilibrium state is distinctly high. As Donnan points out, although it is true that most living cells are larger than the imaginary particle in question, some are not, and probably it does not materially differ in size from phases and parts of cells having separate existence as systems to say nothing of the bacteriophage and ultrafiltrable viruses. "It seems, therefore," he says "very probable that there exist biological systems of such minute dimensions that the laws of classical

thermodynamics are no longer applicable to them. Such laws must be replaced by the statistical theory of molecular fluctuation and in the last resort by the theory of individual action."

It must be noted that to admit this is not to go so far as Johnstone and Lewis, who assert the existence of disentropic phases within the living cell. The question may, moreover, be approached in another way. If a machine, living or otherwise, is perfect it should yield up the same amount of work as is put into it, in other words it should waste nothing of the driving force supplied to it. The ratio between the energy put in and the energy got out may be called the "free energy efficiency" of the process, and obviously for a perfect machine this should be unity or 100 per cent. For a system containing an imaginary being such as Maxwell's demon, capable of defeating the second law of thermodynamics by causing a decrease in entropy the efficiency would be greater than 100 per cent. For all known machines it is less than 100 per cent. The parallel between the numerical figure for the efficiency of living and non-living machines is often very close. To compare the animal to a heat-engine, is, as Guye points out, misleading, for the energy of the steam engine is changed in form as it passes through it, but the comparison between the growing animal and a boiler or an electric battery is much closer. The "apparent energetic efficiency" of the developing embryos of the chick, the silkworm, the minnow, and the frog has recently been calculated (Needham (42)) and works out on the average to 77 per cent. This means that out of 100 gram calories presented to the organism in the form of yolk and white 23 have to be wasted and 77 can be stored. Similarly, the business of the electric accumulator is to store energy and this cannot be done with an efficiency greater than 75 per cent (Davidge and Hutchinson (10)). The boiler, again, is designed to transfer as much heat as possible from coal to steam, but this can never be done with an efficiency greater than 77 per cent (Brownlie (4)). It is doubtful, however, how much stress can be laid on any numerical correspondence between the efficiency of the growing embryo and such non-living machines.

What of course would show up the presence of the Maxwell demon in living matter would be an efficiency greater than 100 per cent. Such an efficiency has never been reported for any of the higher animals under any conditions, but it might be thought that the place to look for it would be the iron and sulphur bacteria, maintaining as they do a precarious existence on the most unpromising foodstuffs. This problem has recently been considered by Baas-Becking and Parks (1). They have calculated the free energy efficiencies of many forms of autotrophic bacteria, and though here, if anywhere, living matter might be expected to need demonic assistance, the efficiencies were always very low. The hydrogen bacteria operated at an efficiency of 26 per cent, the methane bacteria at 30 per cent, the nitrite-forming bacteria at 6 per cent. As for the sulphur bacteria the figure obtained was 8 per cent, and for the iron bacteria (supposing that such organisms really exist) it would also be very low. These observations certainly seem to be in favor of the views of Hill and against the possibility indicated by Donnan and assumed to hold in practice by Johnstone, Lewis, and Driesch. But it must be remembered that an appeal to colonies of bacteria gives no less a statistical result than the appeal to Atwaters' calorimeter. Reference must here be made to a very important recent paper of R. S. Lillie's (34). Lillie

suggests that the existence of rare disentropic phases in living matter, where infractions of the second law can go on might account for the subjective persuasion of freedom which all men have and so introduce a kind of free-will into the structure of science itself. He points out that if such intracellular phases may once with reason be postulated, there is no difficulty in imagining their effect on the body as a whole, in view of the extraordinary capacity which the body has of transmitting changes of state from one point in space to another. In this way a voluntary action would arise from an individual escape from the second law in one of the ultramicroscopic intracellular phases in the living being. But is infraction of the second law the same thing as a breakdown of scientific determinism? Lillie passes by an insensible transition from the latter to the former, but perhaps this is not justified. Does scientific determinism—in so far as it is not confused with scientific naturalism—make any claim to be more than statistical? If in the scientific formulation of things, the individual always escapes, then anything that individual atoms may do in the ultimate recesses of the animal body is metaphysical in the truest and most literal sense of the word.

Lillie himself refers to the expression "physical indeterminism" as a misnomer, and admits that though the laws of the microscopic may not be the same as the laws of the macroscopic, there must be laws of some sort there. And if that is the case, it is difficult to see how on a scientific basis *alone* there can be any spontaneity or freedom. Thus if we suppose that escape from the second law regularly takes place in the intimate structure of living organisms, it will surely not be escape into freedom but into the arms of some wider statistical law inevitably brought into existence by the operation of the scientific way of thought. Or, in other words, the inductive method will again assert its supremacy and nothing will escape from all this save what always did escape, namely, individuality. The unique is the only nut that science cannot crack, and freedom implies uniqueness.

Lillie's paper may be said, then, to push back individuality into the disentropic phase, and not, as its title would imply, to reconcile indeterminism with science. But an altogether fresh wind blows through his memoir in question, and it is significant that he draws attention to the importance of the quantum theory for the philosophy of biology.

Thermodynamical considerations have recently led to the partial solution of one problem which was brought greatly into prominence in neo-vitalistic discussions. The extraordinary fact that the swim-bladder of fishes living at great depths contains nearly pure oxygen was first discovered by Biot (3), who analysed the gas during a scientific expedition and had his eudiometer broken by the explosion. "As nearly pure oxygen" said Haldane (20) "has been obtained from the swim-bladders of fishes living at a depth of 750 fathoms (4500 feet), it follows that oxygen may be secreted into the swim-bladder and retained in it in the gaseous form at a pressure of over 120 atmospheres, whereas the partial pressure of oxygen in the surrounding sea-water is only about one-fifth of an atmosphere. It seems perfectly clear, therefore, that the liberation of oxygen and its retention by the semi-liquid wall of the swim-bladder is the result of an active physiological process in the living cells lining its walls, and cannot be explained mechanically." F. J. W. Roughton (47) has recently suggested that on the contrary

no necessity need be felt for a complete abandonment of mechanical explanation in this case. If the specific heat of the reactants and resultants of a chemical reaction is known, the equilibrium constant can be calculated by the use of Nernst's equation. Now if the equilibrium constant of the reaction $H_2O_2 = H_2O + O$ catalysed by the enzyme catalase be calculated it works out at $10^{18.4}$ from which it may be concluded that not 120 atmospheres but billions of atmospheres would be required to suppress the production of oxygen from hydrogen peroxide by the enzyme catalase. With this most interesting demonstration there collapses one of the most formidable of the objections on which the neo-vitalists have been accustomed to rely. Haldane (21) has recently given a historical review of the famous controversy about secretion and filtration of oxygen in the human lung, and concludes still, as against Barcroft, that only the secretion-theory can explain the facts of acclimatization to life at high altitudes. These questions give additional significance to Roughton's calculation.

REGULATION IN LIVING MATTER

The finalism associated with living beings is nowhere more insistently evident than in their unswerving maintenance of steady states. The living organism has as it were a certain niche in its physico-chemical surroundings, and to that it will always return provided that the disturbing influence has not been so great as to throw it out of gear altogether. Its normal hydrogen ion concentration, its normal osmotic pressure, its normal concentration of glucose or salts, its normal physiological constants, these it will always tend to preserve unchanged. The purposiveness with which it clings to this equilibrium has to be disregarded altogether as such in the application of the scientific method to life phenomena, for teleology is not a concept in any way congruent with measurement. An interesting attempt has indeed been made by Lillie (32) to give biological purposiveness a quantitative expression by regarding it as a special case of equilibrium, namely between organism and environment, and so applying to it an extended form of the principle of LeChatelier. In spite of Lillie's excellent discussion, however, in which the balance between the constructive and constitutive on the one hand and the destructive and dissipative tendencies in living things on the other are so well set forth, it is still extremely uncertain whether the concept of teleology can be translated into mechanical terms. It is more likely that these principles are inherently antipathetic. Probably they cannot with advantage be mixed.

But the phenomena of regulation of steady states in living things may be approached from a purely scientific angle. The importance of buffer action was amply appreciated by Lawrence Henderson, and it will be remembered that in the preface to his book *The Fitness of the Environment* he says that he was led to those considerations by researches on the special properties of solutions of phosphates and borates. Buffer action, indeed, must be regarded as a most important factor in organic regulation. The phenomena of oxidation-reduction potential have been also much studied of recent times, and here again systems have been discovered in which an addition of one of the reactants produces a minimum change in the state of the system as a whole. Such conditions are discussed in the papers of Mansfield Clark and his colleagues (6), and to the phenomenon Clark has given the name "poising action" to indicate its similarity to buffer action in the case of hydrogen ion concentration.

The importance of these advances for the general theory of biology does not seem to have been sufficiently considered. Driesch's expression "a harmonious equipotential system" undoubtedly seemed impossible to imagine on a mechanical basis at the time when he introduced the term, but there is now not the same justification for pessimism. It is becoming clearer and clearer that the living cell exists in an extremely balanced condition, well buffered, heavily poised, apt in every way to resist influences tending to move it out of its equilibrium position. Unsuccessful attempts were made some years ago by L. T. Troland (54) to relate the phenomena of regulation in living cells to the properties of enzymes, but though these failed in detail he was nevertheless on the right track. We may conclude that it is possible, already and in spite of the great incompleteness of our knowledge of biophysics and biochemistry, to point to purely physico-chemical systems that would be bound to exhibit, when working in intimate association, simple forms of that tendency to constancy of internal and external environment which the neo-vitalists regarded as preeminently the god in the machine.

It is worth while also to study in this connection the exact limits of regulation power, for Lillie's question—"Why can the salamander-entelechy regenerate a leg but not the cat-entelechy?" has lost none of its force. In embryology the researches of Spemann and his school, reviewed recently by Huxley (26) and de Beer (2), have done much to clear the air. The totipotence of the early embryo, or rather, the approximation towards the state of totipotence, which is then observed, falls off rapidly as development proceeds, and by the time of gastrulation the process of chemo-differentiation sets in. After this, all development is irrevocably determined, ectoderm cells will make ectoderm and nothing else, until finally in the very late stages regulation of form again becomes possible, owing to the assumption of function; this is the stage of Roux's "struggle of the parts." "The inability of organisms to regulate during the period of self-differentiation of different organs can be illustrated by the analogy of an army," says de Beer, "whose staff at the outset of the campaign has determined and assigned the duties of the various corps. It loses control of these while they are independently performing their allotted tasks, and regains it again later when inter-communication is reestablished. The amazing results of regulation in Clavellina, sea-urchin blastomeres, etc. have led to the forms of vitalism which have been developed by Driesch and others. It is therefore interesting to find that organisms do not always regulate."

MINOR CONSIDERATIONS

An interesting suggestion as to the nature of tonus and trophic action in living organisms has recently been made by Sir W. B. Hardy (22). The manner in which nerve fibres control tonus and heat-production in muscle, for instance, has always been exceedingly obscure and has furnished a theme for several neo-vitalist physiologists. It is indeed true that while we have considerable information about the waves of nervous excitation which produce muscular movement, we know nothing at all about the nature of trophic action and the control of tonus in muscle. Hardy suggests that the explanation may probably be found in the orientation of molecules, a process which can certainly happen in masses of matter though it has been mostly studied in surface films. Experiments with lubricants demonstrate that layers of ori-

ented molecules may be several thousands thick, and though this is, as Hardy says, an insignificant example beside the colossal ones furnished by the living organism, yet it is the first likely explanation of trophic action that has been advanced and thus removes from physiology the stigma of having absolutely no explanation at all for such phenomena.

Reference may also be made to the monograph of Hedges and Myers (23), who have collected together a great deal of information about periodical reactions in pure chemistry; reactions which exhibit rhythmic pulsation or intermittency. The most famous example of such a reaction is probably the formation of the Liesegang rings. This book forms the most considerable addition of recent times to the literature concerning "simulacra vitae," already very considerable in extent. Although it is true that from a philosophical point of view the significance of these imitations of living processes can easily be overestimated, yet they have a certain value, and the more they accumulate, and the more complicated they become, the more difficult it is to hold the views of Haldane, Driesch, or Rignano. It is much to be wished that some historian would collect the many data in existence about "simulacra vitae" beginning with Roger Bacon's speaking head and passing through the automaton chess-players of the time of de la Mettrie to the selenium dog and Lotka's mechanical beetle.

Finally, a word might be said with advantage about the supposition that the biologist is always, if the truth were told, a thanatologist and that biophysics and biochemistry are simply the study of dead matter which had once been alive. This belief is common; for example, Johnstone (29) says "Remember the (easily ignored) fact that of living substance we literally know nothing. We study the behavior only of the living organism. Whenever we study organic substance, it is necessarily dead inert material that we investigate." Such inaccurate statements may surely cause great misapprehension in the minds of laymen. Physiology and biochemistry have never been restricted to examining dead animals, and as technique develops they do so less and less. As instances the work of Chambers (5) and others (45) might be given, in which indicators are injected into living cells, or Gelfan's (15) micro-electrodes used in a similar manner, or again, Seifriz's (48) determination of protoplasmic viscosity by means of an exceedingly minute metal ball introduced into a single cell and then caused to move towards an electro-magnet. Vlès (55), moreover, has determined the intracellular pH by spectroscopic and spectrophotometric methods involving no interference with the living cell at all. The constitution of plant tissue has been examined with x-ray analysis by Sponsler (50), and Crozier (8) has shown what far-reaching conclusions about the metabolism of living animals can be drawn from a study of the effects of temperature upon them, as may also be seen from the beautiful work of O. Glaser (16), which caused no greater inconvenience to his paramoecia than getting them to swim through a glass tube at different temperatures. There can be no doubt that as biological methods become more refined, the injury caused to the experimental material will become ever slighter.

CONCLUSION

It will not be very difficult to outline shortly the direction which the trend of thought in the philosophy of biology is at present taking. The neo-vitalist school, which some years ago seemed to

have the future in its own hands, has not been able to live up to its promises. The more its special entities immanent in living beings have been considered, the less necessary they have seemed to be in relation to the facts and the less valuable they have been found as inspirations to research. The finalist school with its insistence on teleology as the special sign-manual of life has been unable to deny the teleology of the inorganic world, so that the Aristotelian conception modified by Kant of the efficient cause and the final cause as two complementary explanations of all natural phenomena remains unsuperseded. The older organicism, which saw in living organisms an interrelatedness of parts present nowhere else in the universe, has been swallowed up in an organic theory of nature which regards all things, and even all events, as themselves organisms. The classical biological mechanisticism with its roots invisibly but surely embedded in the naturalistic view of the world has withered away altogether since the general abandonment of the notion that the application of the scientific method exhausted the content of things. And lastly, the psychobiologists, who asserted that biology could only be made intelligible by employing psychological concepts at all points, have failed to commend their views by producing a serious body of experimental work.

Out of the decay of these theories—valuable as they certainly were in their day—have arisen various standpoints one of which has come to be called "Neo-mechanism" (43). It is represented by a variety of biologists and others (53, 37, 9, 28, 33, 36, 35, 46, 49, and 51) who all agree in regarding the scientific method as essentially mathematical, mechanical, deterministic, quantitative, abstract, and by consequence inapt to include the entelechy or any similar conception; and with all this, at the same time a partial, distorted, and as it were twisted approximation to truth. The neo-mechanistic position, therefore, at one and the same time asserting the universal dominion of the mechanical sort of explanation over all nature, living and non-living, and admitting the inadequate nature of this sort of explanation as a full account of the world, resembles the old mechanisticism in maintaining the heuristic need for the machine, and differs from it in seeing nothing solely ultimate about the machine. It thus recognizes itself to be the way the scientific mind goes to work, and not the manner of thinking in philosophy, theology, or art. It differs of course completely from neo-vitalism in denying the bare value of any entelechy or archaeus in living things; it can have nothing to do with any elasticity in its laws, and deprecates that παρέγκλισις which Lucretius was weak enough to introduce into his world.

> " . . . . incerto tempore ferme
> incertisque locis spatio depellere paulum,
> tantum quod nomen mutatum dicere possis."

It also differs from biological finalism, for it knows teleology to be an unquantitative category, and banishes it from the laboratory to the domain of the philosophers, who are quite capable of dealing with it. It welcomes the organic theory of nature, for to the exact biologist, nothing is an organism any more than anything else; to the philosopher, all things are organisms, and just as the scientific mind sees different degrees of complexity in its systems, so the philosopher sees emergent degrees of complexity in his organisms, up to the world-soul itself. The neo-mechanistic position stands in close relationship with the views put forward by R. G. Collingwood in his recent book

Speculum Mentis (7), and for a statement of the theory of science here adopted, the chapters on science in his work are much more than adequate. It is easy to see how the experimental advances which have been collected together in this paper fit in with the neo-mechanistic attitude. The organic theory of nature, which seems to have so great a future before it, is the natural counterpart in philosophy of neo-mechanism in biology and what we know of the thermodynamic aspects of living things gives us little reason for supposing that the laws we have now are likely to break down in biology in the future. Neo-mechanism gives biological science all it wants and at the same time is not easy to attack from a philosophical angle, for the simple reason that it makes no philosophical claims.

It may be noted that such a standpoint will not necessarily object to special "biological" laws or explanations, provided that these are clearly understood to possess an "interim" character and to be only awaiting expression in physico-chemical terms. There is no harm in classing the poppy with other therapeutic plants as having the "virtus dormitiva" of Galen and of Molière, provided Overton's theory and all its more accurate successors follow close behind. To say that opium possesses a "dormitive faculty" is a mere restatement of the facts but to say that it does so because morphine is fat-soluble is at least intelligible even though it may not be true. It promises truth to come. But this is not to admit the value of "special biological laws" conceived in terms of "activity, purpose, values" etc. and never intended to be reduced to physico-chemical intelligibility. Such generalizations as these still find defenders, e.g. J. H. Woodger (57). "Because mechanics," he says, "quite rightly banishes 'force' and 'activity' from its conceptual equipment as mere anthropomorphism, is it correct to turn this deanthropomorphizing process on ἄνθρωπος himself?" The answer is yes, if ἄνθρωπος is to be an object of scientific study, for a strenuous tendency against projections of ourselves into the external world is one of the principal characteristics of the scientific method. There exists here a confusion of philosophy and perhaps theology also with science which has caused much trouble in the past and will cause more. Ἄνθρωπος not deanthropomorphized is a mixture of all kinds of experience, exact biology, philosophic speculation and argument, religious and artistic appreciation, historical understanding. In so far as he is the object of scientific thought, he must be deanthropomorphized: and the legitimate aversion to paradoxes which we all feel kept within bounds.

If, then, for the biologist neo-mechanism seems to fit in best with recent tendencies in the theory of the study of living things, the future becomes clearer than before. There is nothing save the inherent difficulties of research to hinder the advance of exact physico-chemical methods in biology, and these obstacles have never yet daunted the enthusiasm of investigators. It was the paper lions of vitalism in their path that made them hesitate; the fruit of minds overprone to regard as inexplicable that which has not been explained. At the same time, the frank rejection of that philosophy which regarded the scientific method as the only one capable of revealing truth establishes the claim of modern biology to metaphysical respectability. Biology can claim to be well aware of the limitations inherent in the method of science, and of the illimitability of the subject-matter to which it can be applied.

James Johnstone, in a recent paper

(30), has adopted the neo-mechanistic position, which is all the more surprising in that his former works could accurately be described as a "skilful blend of Driesch and Bergson." But now he says "It is a plain and very obvious fact that we have built up our societies and social relationships on the basis of quite irrational recognitions of life in other things than ourselves, and it is very curious that we should refuse to consider this experience as part of that which can be explained in physical terms. Yet it is quite certain that biology will never abandon its mechanistic attitude. The latter is something more than merely an hypothesis, it is a demand or an ideal of explanation which we insist upon in our investigation of life activity." It is, in a word, one of the fundamental ways in which we think, and its apriority is something which we cannot possibly get behind. "Mathematics, mechanics, and materialism," as R. G. Collingwood puts it, "are the three marks of all science, a triad of which none can be separated from the others, since in fact they all follow from the original act by which the scientific consciousness comes into being, namely, the assertion of the abstract concept." But science is not the only activity of the human spirit.

There is indeed all the difference in the world between pushing mechanistic explanation as far as it will go with the realization that it will go all the way but will not entirely satisfy you when you have got there, and diluting it with other (qualitative) sorts of explanation, in the hope that the mixture will afford you full satisfaction. It is this latter process that is being given up in biology. Scientific explanation and philosophical explanation are two distinct foods of the soul, and they are confused only at great peril. Or, in the words of an immortal limerick due to Charles Inge,

"There was an old fellow of Crediton,
Who took paté-de-fois-gras and spread it on
A chocolate biscuit
Exclaiming 'I'll risk it!'
His tomb gives the date that he said it on."

LIST OF LITERATURE

(1) Baas-Becking, L. G. M., and G. S. Parks. Physiological Reviews, 1927, 7, 85.
(2) de Beer, J. R. Experimental Embryology. Oxford, 1926.
(3) Biot, J. B. Mémoires de la Société d'Arcueil. 1807.
(4) Brownlie, D. The Electrician, June 29, 1923.
(5) Chambers, R. Journ. Gen. Physiol., 1927.
(6) Clark, W. M., *et alia*. Reports of the U. S. Pub. Health Service, Reprints Nos. 823, 826, 834, 848, 904, 915, 1017.
(7) Collingwood, R. G. "Speculum Mentis." Oxford, 1926
(8) Crozier, W. J. Journ. Gen. Physiol., 1925–27.
(9) D'Arcy, C. F. Science and Creation. 1925.
(10) Davidge and Hutchinson. Technical Electricity, p. 252.
(11) Delage, Y. L'Hérédité et les grandes problèmes de la Biologie. 1903.
(12) Donnan, F. G. Journ. Gen. Physiol., 1927, *8*, p. 685.
(13) Driesch, Hans. Science and Philosophy of the Organism. 1912, 2, p. 202.
(14) Frankland, P. F. Nature, 1898, *59*, p. 30.
(15) Gelfan, S. Publ. Biol. Univ. of California. 1926.
(16) Glaser, O. Journ. Gen. Physiol., 1926.
(17) Guye, C. E. Arch. des Sci. Phys. et Nat., 1920.
(18) ———. Physico-Chemical Evolution. 1925.
(19) Haldane, J. S. Organism and Environment as Illustrated by the Physiology of Breathing. 1917.
(20) ———. The New Physiology. 1919.
(21) ———. Physiological Reviews, 1927, 7, p. 363.
(22) Hardy, W. B. Journ. Gen. Physiol., 1927, *8*, p. 641.
(23) Hedges, E. S., and J. E. Myers. The Problem of Physico-Chemical Periodicity. 1926.
(24) von Helmholtz, H. Wiss. Abhandlungen., 1883, *2*, p. 972.
(25) Hill, A. V. Thermodynamics in Physiology. Manchester Memoirs, 1924, *68*, p. 32.

(26) HUXLEY, J. S. Nature, February 23, 1924.
(27) JAPP, F. R. Nature, 1898, *58*, p. 616.
(28) JENKINSON, J. W. Studies in the History and Method of Science. 1911, p. 59.
(29) JOHNSTONE, J. The Mechanism of Life. 1921.
(30) ———. Journ. Phil. Studies., 1926, *1*, p. 183.
(31) LEWIS, G. N. The Anatomy of Science. 1927.
(32) LILLIE, R. S. Journ. Phil. Psych., and Sci. Meth., 1915, *12*, p. 589.
(33) ———. Journ. Phil. Psych., and Sci. Meth., 1926, *23*, p. 673.
(34) ———. Science, N.S., 1927, *66*, p. 139.
(35) MARSHALL, H. R. Mind, 1902, *11*, p. 470.
(36) McDOUGAL, R. Science, N.S., 1913, *37*, p. 104.
(37) MEYER, A. Logik der Morphologie. 1926.
(38) MORGAN, C. LLOYD. Life, Mind, and Spirit. 1926, p. 66.
(39) ———. Proc. Aristotelian Soc., February 14, 1927.
(40) MURRAY, C. D. Proc. Nat. Acad. Sci., Washington, 1926, *12*, pp. 207 and 299.
(41) ———. Journ. Gen. Physiol., 1926, *9*, p. 835.
(42) NEEDHAM, J. Brit. Journ. Exp. Biol., 1927.
(43) NEEDHAM, J. Hibbert Journal, 1927, *25*, p. 265.
(44) ———. Man a Machine. Psyche. Miniature Series, 1927.
(45) NEEDHAM, J. and D. Proc. Roy. Soc., 1926.
(46) OGDEN, R. M. Journ. Phil. Psych. and Sci. Meth., 1925, *22*, p. 281.
(47) ROUGHTON, F. J. W. Paper "The use of thermodynamics in biology," to the Cambridge Biochemical Club, in May 1927.
(48) SEIFRIZ, E. Brit. Journ. Exp. Biol., 1925, *1*.
(49) SONNEBERG, W. The Monist, 1918, *28*, p. 585.
(50) SPONSLER, O. L. Journ. Gen. Physiol., 1925.
(51) SUMNER, F. B. Journ. Phil. Psych. and Sci. Meth., 1910, 7, p. 309.
(52) THOMSON, W. Proc. Roy. Soc. London, 1852.
(53) TRIEPEL, F. Die Zweite Schicht des Denkens in der Naturwissenschaft und Leben. 1926.
(54) TROLAND, L. T. The Monist, 1914, *24*, p. 92.
(55) VLÈS, F. cit. in P. Reiss. Le pH intérieur cellulaire. 1926, p. 134.
(56) WHITEHEAD, A. N. Science and the Modern World. 1926.
(57) WOODGER, J. H. Sci. Prog., 1927, *21*, p. 697.

CEPHALOPOD ADAPTATIONS—THE RECORD AND ITS INTERPRETATION

By EDWARD W. BERRY

Department of Geology, Johns Hopkins University

IT SHOULD be recognized at the outset that the present paper is highly speculative in character. Not that the author has much faith in such a method of attacking a problem, but, as will appear in the sequel, because this is the only method of approach in any consideration of the probable structure of the soft parts or habits of life of the extinct representatives of this very important class of the Mollusca.

The abundance of fossils of this class in the English midlands, where William Smith first developed the idea of stratigraphic succession, their similar abundance in the historic eastern Alps and elsewhere in Europe near centers of scientific population, early stimulated speculation regarding the characters of the inhabitants of these fossil shells, and so much has been written upon this subject that it is doubtful whether any of the ideas advanced here have not already been proposed in one form or another. I have tried to acquaint myself with the literature, but will not attempt citation in most cases, contenting myself with the foregoing disclaimer of originality.

The Cephalopoda, whose ancient line extends over at least a hundred million years from the oldest known forms of the Cambrian period to the present, and which easily comprises upward of 10,000 known extinct species of great variety of form and presumably of habits, is represented in existing seas by a single restricted (Willey, 1902, recognizes four species) genus with an external shell—the familiar pearly Nautilus; by the less known monotypic genus *Spirula*, with an internal shell; by the variety of active squids and cuttles, with an internal highly modified vestige of a shell; and by the less active octopus tribe, without any trace of a shell.

Throughout the greater part of the geological record their representation in the rocks will naturally be the shelled forms, which alone furnish the requisite hard parts for normal preservation as fossils. Among these the great group of ammonites, with their highly specialized septa, have been entirely extinct since Cretaceous time. (I do not think that I need waste space in refuting Steinmann's idea that the existing dibranchiates are their direct descendants.) The racial history of the ammonite order extended from the late Silurian to the close of the Upper Cretaceous—an inconceivably long period, during which they developed a multitude of forms, and they were easily the dominant cephalopods throughout much of the Mesozoic era.

Since the existing shell-less forms are geologically modern and show every indication of post-Paleozoic evolution culminating in modern times, they afford but slight basis for comparison with the multitude of shelled forms that go back to the oldest fossiliferous rocks. The

existing Spirula, which is itself related to the ancestral squids, is quite unlike the remote shelled ancient stock; so that the existing Nautilus alone can serve as a point of departure from which to envisage the structure and habits of the majority of fossil forms.

This lack of existing comparable forms has led to serious misinterpretations of extinct forms, stratigraphic and taxonomic paleontologists usually not having seen the forest because of the trees, and has opened the way for a multitude of diverse speculations and generalizations, more often dogmatic than probable. It is proposed in the following pages to pass in review what may be logically inferred regarding the structure and habits of these long vanished races, and it is freely admitted that a single fact of observation may upset a sheaf of deductive philosophy.

CEPHALOPOD CLASSIFICATION

Richard Owen, who gave us an admirable account of the anatomy of the pearly Nautilus in 1832, divided the existing cephalopods into two sub-classes—the two-gilled, shell-less Dibranchiata, and the four-gilled Nautilus or Tetrabranchiata. Paleontologists have rather generally assumed that the extinct nautiloids and ammonoids had four gills as in the single surviving genus *Nautilus*, although the two-gilled forms were obviously derived from the same stock. This assumption is highly illogical and equally improbable. It is not a matter of great moment whether the extinct forms had two, four, or some other number of gills—there is a great amount of diversity in this feature throughout the molluscan phylum; but it is important, it seems to me, not to base their segregation into major groups upon the number of gills when we can never hope to know what the number was in 99 per cent of the cases. The sub-classes of Owen are therefore meaningless throughout all time but the present. The alternative terms Ectocochlia and Endocochlia for the two classic sub-classes are not particularly euphonious, fail to recognize the threefold diversity of the cephalopods, and are most inappropriate, since a considerable number of the Endocochlia lack all traces of a shell, and others—the extinct belemnoids and the existing Spirula—are ectocochlia in their youth and become endocochlia during their ontogeny.

Three subclasses should be recognized, namely: the Nautiloidea, Ammonoidea, and Coleoidea or Dibranchiata—the last largely living, and the fossil forms furnishing enough indications of their soft anatomy in the fine grained muds of the Jurassic to give a fairly clear idea of their structure.

A second rather general misconception of another morphological feature of the extinct animal has been the assumption that since the pearly Nautilus has numerous tentacles, all fossil nautiloids and ammonoids were similarly equipped. We know that in *Spirula*, the existing squids and Octopoda, and the extinct belemnoids, quite a different and more restricted number of more specialized tentacles was universally present, and since these groups were derived from the more primitive shelled stock, the question of whether fossil nautiloids and ammonoids had many tentacles or a few so-called arms is to be determined, if at all, by evidence drawn from the geological record and not from their supposed position in the taxonomic scheme of the systematists.

The keynote of evolution of the hosts of extinct cephalopods, as it appears to me, is adaptation—a thought already ably voiced by Diener. The founders of the more modern study of fossil cephalopods—men like Alpheus Hyatt—were entirely

dominated by a sort of theological philosophy, and particularly by one of the outstanding tenets of the American school of Neo-Lamarckianism, namely: that of racial senescence as expressed in seemingly bizarre appendages or ornamentation, and supposed atavistic simplification of the shell architecture. What could seemingly be more conclusive evidence of senescence than *Baculites*, appearing near the close of the geological record of the ammonites, with its tiny coiled baby shell like that of its ancestors, early forsaking the ancestral plan of rectitude and straightening out into a large orthocone? It would even have an immoral quality in the mind of the late John M. Clarke.

However, since racial senescence, in the sense that the protoplasm, vital force, nucleic control, or whatever you choose to call it, had suffered an old-age devitalization which was responsible for the observed changes in form, is non-existent, some other explanation must be sought, and my answer would be that this was adaptation to new environments or habits. Racial senescence is only permissible as a descriptive phrase for a race, not necessarily old, which is not overly successful in competition with its contemporaries and is therefore dwindling. Such a one, and there are many throughout the history of all fossil groups, is more appropriately compared with a backward human race than with a senile individual. In any case the use of the phrase is not the explanation of the observed changes of form or ornamentation that the fossil record discloses.

THE EVOLUTION OF THE CEPHALOPODS

In the following pages I shall endeavor to give a very much abridged account of the evolution and adaptation of the group, and then discuss a few selected examples in somewhat more detail. To attempt a complete survey of a group containing as many described species as all the known mammals—both recent and fossil—would be to write a book, and probably to obscure the subject. The general phylogenetic relations of the different groups and a simplified epitome of their geological history are shown on Plate 1.

Malacologists are rather generally agreed that the archetypal stock of all of the Mollusca could not have differed greatly from the synthetic form which E. Ray Lankester constructed many years ago, and such a form is shown in longitudinal section in Plate 2, figure 1, in which the shell, visceral cone, course of the alimentary canal, and crawling foot are differentiated. Such a form might readily give origin to gastropod, scaphopod, lamellibranch, or amphineuron. To become an incipient cephalopod it would have merely to narrow the aperture of the shell, heighten the cone, and cut off its apex by septa. How this came about I shall consider presently.

At this point it is necessary to correct another misconception of the soft parts. When the short body of the pearly Nautilus is compared with that of a more active squid the proportions are in striking contrast, and it has been tacitly assumed that the extinct shelled species had bodily proportions comparable to those of the Nautilus. Many had, or were even shorter; others had not, and were quite as elongated as a squid or even longer. Examples can be cited at almost any time during geological history. For instance, the cigar-shaped body of the immature *Proterocameroceras brainerdi* (Whitfield) of the Ordovician was eight or nine times as long as it was wide.

Other early nautiloids with elongated bodies were the genera *Ophidioceras* (fig. 13), *Schroederoceras* (fig. 12), *Deltoceras*, *Piloceras*, *Vaginoceras*, *Lituites*, etc. Among the later ammonoids the genus *Macro-*

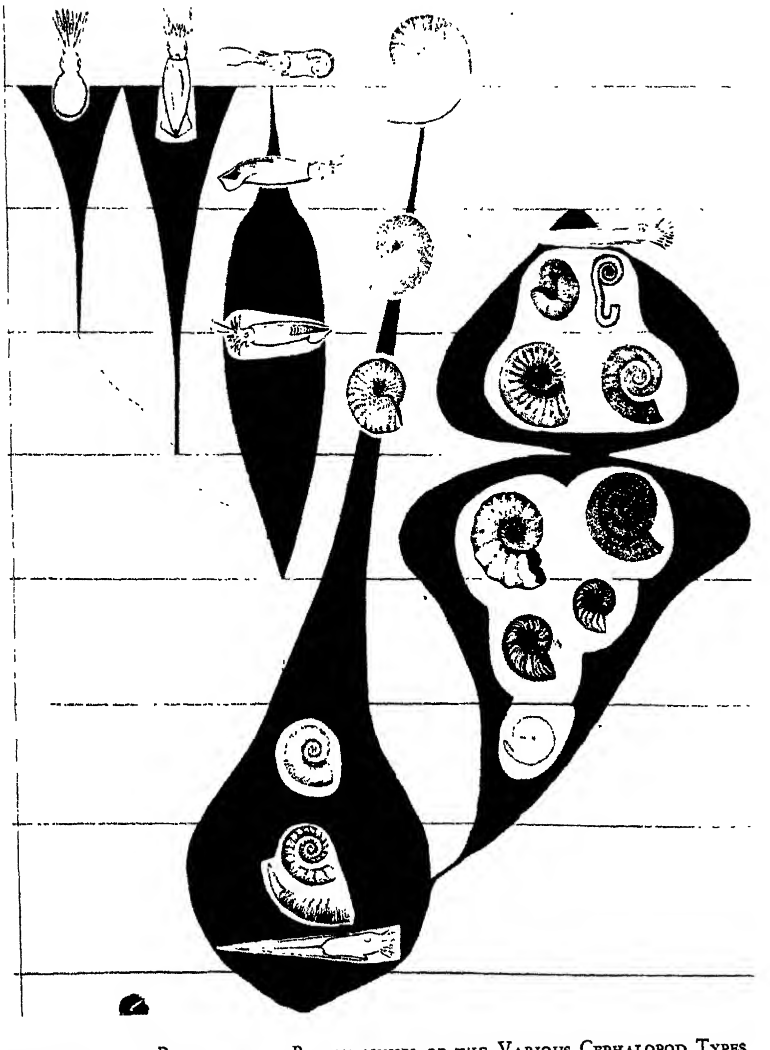


Diagram Illustrating the Phylogenetic Relationships of the Various Cephalopod Types, their Range in Time, and Relative Representation in the Past

At the left is the life-line of the relatively modern Octopoda; the next life-line is that of the somewhat more ancient and less specialized Decapoda; the next is that of the Belemnoidea, which reached their maximum during the Mesozoic and are represented in existing seas by *Spirula;* the next is that of the Nautiloidea, which reached their maximum in the earlier Paleozoic. The right hand life-line is that of the Ammonoidea, which appeared in the record in the late Silurian, reached an early maximum of differentiation in the Triassic, became nearly extinct in the late Triassic, rapidly attained a second maximum in the Jurassic and became extinct with the Upper Cretaceous.

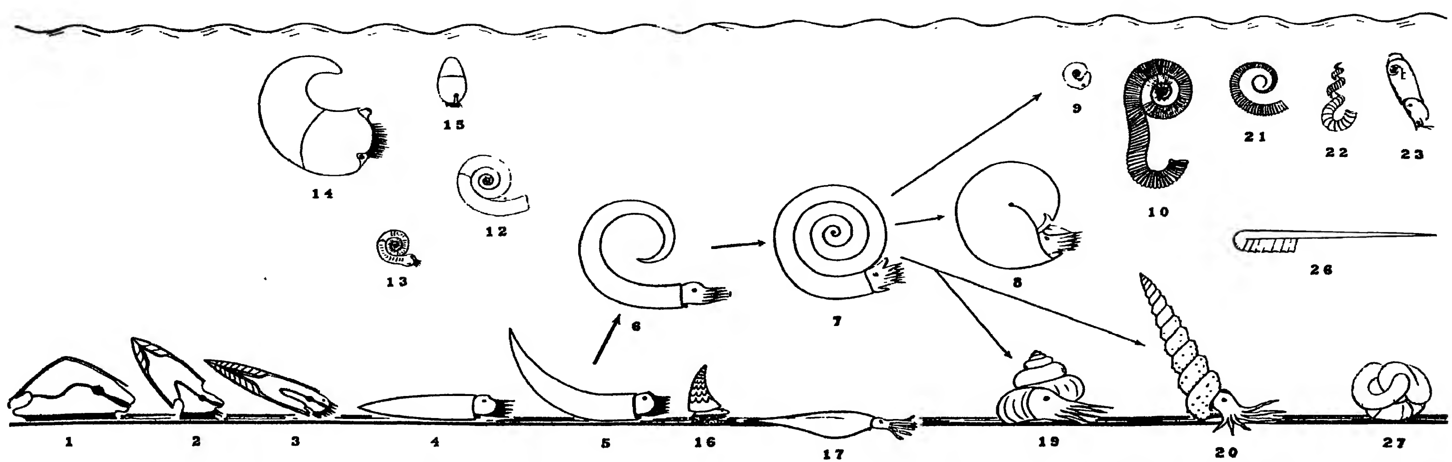


DIAGRAM ILLUSTRATING THE ADAPTATIONAL MODIFICATIONS OF THE CEPHALOPODA WITH EXTERNAL SHELLS, TO BE READ FROM LEFT TO RIGHT. BENTHONIC FORMS AT THE BOTTOM, NECTONIC FORMS IN THE MIDDLE, AND PELAGIC FORMS AT THE TOP

FIG. 1. The Molluscan archetype, hypothetical. (After Lankester.)
FIG. 2. Elongation and contraction of cone, partial transformation of the foot, hypothetical.
FIG. 3. More advanced stage of preceding, hypothetical.
FIG. 4. Horizontal Orthoceras stage.
FIG. 5. Cyrtoceras stage.
FIG. 6. Gyroceras stage.
FIG. 7. Fully coiled stage.
FIG. 8. Involutely coiled stage.
FIG. 9. *Morphoceras pseudoanceps* Douvillé, a pelagic Jurassic ammonite with partially closed aperture. (Bajocian of France, after Douvillé.)
FIG. 10. *Macroscaphites ivani* (d'Orbigny), a Lower Cretaceous non-swimming ammonite. (Barremian of France, after d'Orbigny.)
FIG. 12. *Schroederoceras eatoni* Whitfield, an Ordovician partially floating nautiloid. (Fort Cassin beds of New York, after Ruedemann.)
FIG. 13. *Ophioceras simplex* Barrande, a Silurian partially floating nautiloid with constricted aperture. (Étage E of Bohemia, after Barrande.)
FIG. 14. *Phragmoceras inflexum* Hedström, an endogastric prevailingly floating Silurian nautiloid with constricted aperture. (Silurian of Gotland, after Hedström.)
FIG. 15. *Mandaloceras bohemicum* (Barrande), a pelagic Silurian nautiloid with constricted aperture. (Étage E of Bohemia, after Barrande.)
FIG. 16. *Cyrtoceras parvulum* Barrande, a representative of the breviconic small forms which retained the primitive crawling foot as late as Silurian time. (Étage E of Bohemia, after Barrande.)
FIG. 17. *Gonioceras*, representing a group of greatly depressed benthonic crawlers. (After Ruedemann.)
FIG. 19. *Turrilites robertianus* d'Orbigny, a Lower Cretaceous benthonic crawler. (Albian of France, after d'Orbigny.)
FIG. 20. *Turrilites tuberculatus* Bosc. Another late Lower Cretaceous benthonic crawler. (Albian of France, after d'Orbigny.)
FIG. 21. *Spiroceras bifurcatum* (Quensted), a Jurassic feebly swimming and floating ammonite (Callovian of Würtemberg, after Quensted.)
FIG. 22. *Heteroceras reussianum* d'Orbigny, an Upper Cretaceous pelagic ammonite. (Emscherian of Germany, after E. Fraas.)
FIG. 23. *Spirula australis* Lamarck, floating position. (After Chun.)
FIG. 26. *Ptychoceras puzosianus* d'Orb., a Lower Cretaceous swimmer. (Neocomian of France, after d'Orbigny.)
FIG. 27. *Nipponites mirabilis* Yabe, a sessile Upper Cretaceous form from Japan. (After Yabe.)

scaphites (fig. 10), the family Lytoceratidae, and numerous others, show a similar elongation of the body chamber.

Without attempting a detailed explanation, it may be noted that in either swimming or passively floating forms there seems to be a direct correlation between the weight of the body and the buoyancy of the empty chambers of the shell, calculated to maintain the animal in a normally functional position according to its habits. This may seem like reasoning in a circle, but I shall try to show in a few selected cases that it is not.

Plate 2, figure 2 shows a hypothetical stage in which the shell had become partially elongated and contracted, the visceral cone was correspondingly narrowed, and a few partial septa, lined internally with horny endocones, had developed, much as in the family Endoceratidae of the Ordovician and Silurian periods, though not in such an advanced manner as in that family. The shell had not yet developed enough air chambers to be appreciably buoyant, and the foot had shortened progressively, although still possessing a partially functional crawling surface; its anterior portion had commenced to encircle the mouth, and to assume tactile and prehensile functions.

Plate 2, figure 3 shows a second, more advanced hypothetical stage, with a still narrower and more elongated shell and visceral cone, and more numerous septa. The foot is almost entirely transformed into tentacular segments, which completely encircle the mouth; its hinder portion has the two reduced lateral halves appressed, much as in the taxodont genus *Nucula*, and this part becomes the incipient swimming siphon or hyponomic funnel.

In Plate 2, figure 4 we pass from the hypothetical to the actually observed Orthoceras form with which it is customary to start cephalopod phylogeny. The most obvious feature, giving its name to this type, is that the shell is an orthocone, or straight cone. However, a more searching study of the orthocones that are so abundant in the older Paleozoic rocks shows the greatest amount of variety in the details of structure, and is clearly indicative of a like variety of habits of life. When we recall that orthocones swarmed in the older Paleozoic seas, and largely filled the rôle of the fishes of later times, we are bound to admit the probability of their having become adapted for every possible environmental niche. Some were sluggish, others active; some were benthonic, crawling on the sea bottom; others nectonic or swimming forms; and still others may have been planktonic, floating on the surface. They ranged in size from that of a lead-pencil to giant forms a dozen feet or more in length. (Certain species of *Endoceras* are said to have attained a length of 15 feet.) Their siphuncles were tiny to excessively large, and variously modified; their early chambers were empty or filled to various degrees with organic deposits; some fashioned accessory chambers far forward on top of the adult living chamber, whose buoyancy enabled them to maintain an even keel (See Plate 3). I shall return to some of these modifications of the orthocones and their probable interpretation after following the general course of evolution of the whole group on through to the attainment of the enrolled shells so typical of the late Paleozoic and succeeding Mesozoic era.

PROGRESSIVE COILING OF THE SHELL

If one single feature may be said to characterize the phylogeny of the shelled cephalopods as a whole, it is that of progressive coiling. The older naturalists found a supposed reason for this in the phrase "natural selection favored the

compactly coiled shell," but as Dunbar has pointed out, this explanation, like so many of the natural selection sort of explanations, fails to explain why, or to take into account the intermediate curved (cyrtocone) and incipiently coiled (gyrocone) stages, and this same author, adopting Buckman's idea (1919), has elaborated the true reason, namely: that progressive coiling is an adjustment to the buoyancy of the empty chambers of the shell which induced it.

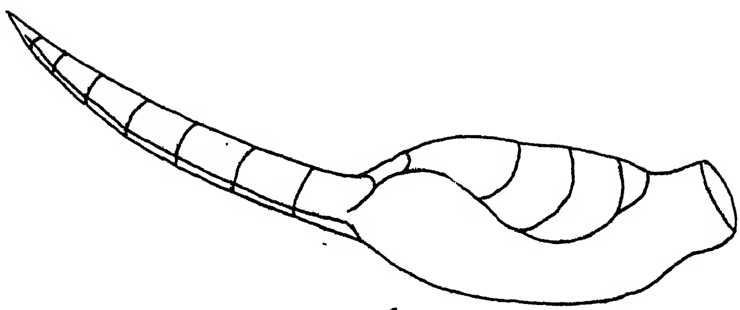
The older naturalists, commencing I believe with Buckland in 1835, believed that the early chambers of the shell served for hydrostatic purposes, a belief due in the first instance to one of the few mistakes in the account of the anatomy of *Nautilus* given by Owen, who described the axial canal of the siphon as forming a communicating conduit between the empty chambers and the mantle cavity. When the animal wished to descend, these chambers were filled with water; when it wished to rise they were emptied—exactly on the operative principle of a submarine. This idea is perpetuated in the last edition of Eastman's Zittel (1913, p. 589), although Dean's (1901) observations on the identical buoyancy in the living and dead Nautilus and Willey's (1902) demonstration that the siphon does not communicate with the mantle cavity in *Nautilus* should set at rest the hydrostatic myth. The empty chambers in *Nautilus* are buoyant once for all, and what is true in this respect for *Nautilus* should apply to all of the extinct camerated forms that did not fill the early chambers with organic deposits.

This buoyancy of the unfilled earlier chambers is the keynote to the observed changes in shell form, in both phylogeny and ontogeny, and the merit of first applying it in any detail belongs to Dunbar (1924).

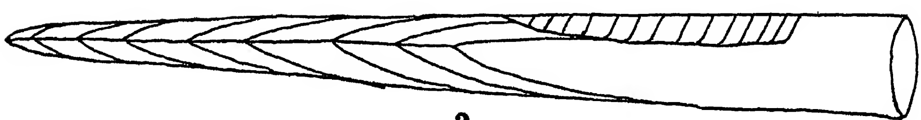
With the formation of complete septa shutting off the apical chambers in the developing orthocones, their buoyancy in those forms that did not weight this end by organic deposits filling the chambers or elaborate deposits about the enlarged siphuncle would tend to tilt the shell forward. Such a tilting would be a handicap in either a nectonic or benthonic animal. Whether the resulting tension on the ventral side would cause a more rapid growth of the ventral shell margin, or whether normal secretion of the animal in so orienting its body as to keep its mouth out of the mud of the bottom or to remain horizontal in the water would be the predominant factor cannot be decided. In any event, the more rapid growth on the ventral side would result in an arcuate shell—the cyrtocone (Plate 2, fig. 5), and the more the curvature, the more the forward migration of the center of gravity would be retarded.

This finally resulted in the gyrocone type of shell (Plate 2, fig. 6). The progressive coiling would not stop with this type since, as the shell is an expanding cone, the newest chambers immediately behind the living chamber, with their exterior position and much increased volume, would throughout adolescence tend to tilt the animal forward, and this would eventually result in the coiled type of shell known as an ophiocone (Plate 2, fig. 7). Complete equilibrium with the animal in a horizontal position most effective for swimming is only attained when the later chambers entirely invest the earlier whorls as in the existing *Nautilus pompilius*, a completely involute form. Or an ophiocone may attain the same stability if there are many volutions to the shell, which serves to explain the persistency of the latter type.

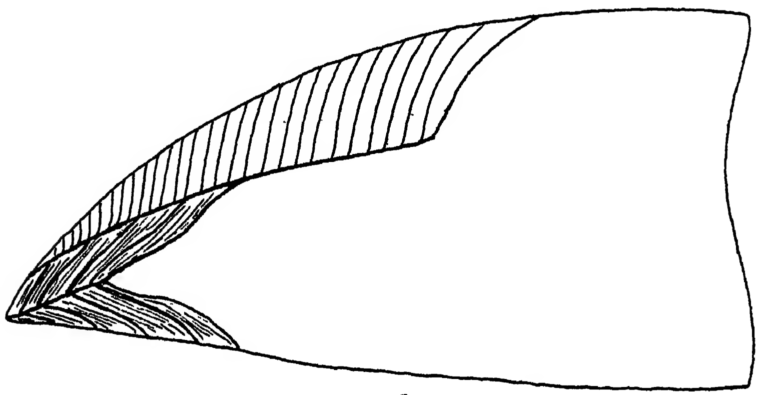
The foregoing simplified series of stages, illustrated by figures 1–8 of Plate 2, is



1



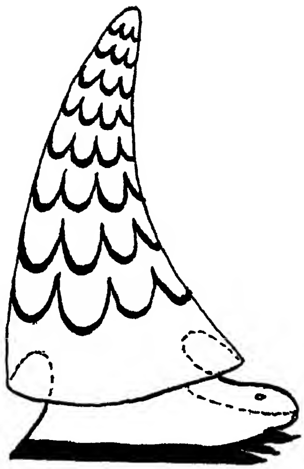
2

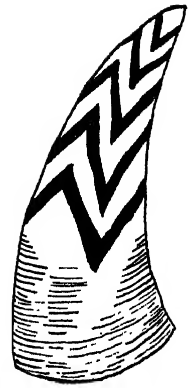


3

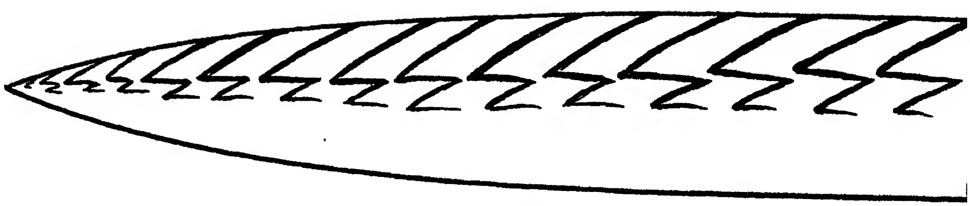
FIG. 1. *Ascoceras*, based upon *Ascoceras bohemicum* Barrande, from the Silurian of Bohemia.
FIG. 2. *Proterocameroceras brainerdi* (Whitfield). Ordovician of New York. (After Ruedemann.)
FIG. 3. *Piloceras*. (After restoration by Ruedemann.) An Ordovician type.
All in median longitudinal section.

1

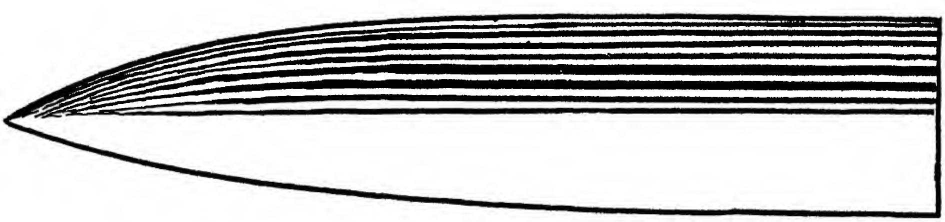




3



4



5

Color Pattern and Attitude among the Early Nautiloids

Fig. 1. *Cyrtoceras fallax* Barrande. Silurian of Bohemia.

Fig. 2. *Cyrtoceras parvulum* Barrande, showing color pattern and restoration of soft parts. Silurian of Bohemia.

Fig. 3. *Cyrtoceras decurio* Barrande. Silurian of Bohemia.

Fig. 4. *Orthoceras anguliferum*. Middle Devonian of Germany. (After Dunbar.)

Fig. 5. *Geisonoceras tenuitextum* (Hall). Middle Ordovician of New York. (After Ruedemann.)

an epitome of the general and normal trend of evolution in the shelled cephalopods. The end product would be a nectonic animal with greater or less locomotive powers—as were the majority of shelled forms. But there are a host of exceptions to this general trend, as there necessarily must have been if these animals were to adapt themselves fully to the varying environments of the seas—as they undoubtedly did.

LIFE HABITS OF THE ORTHOCONES

In considering these modifications we may first consider the variations shown in the early orthocones. Fully half of the known Ordovician cephalopods had shells which were orthocones. Speculations as to their habits of life have been more fantastic and mutually exclusive than is the case in any of the later cephalopods. They have been pictured as swimming in both vertical and horizontal attitudes, as having dragged their horizontal shells over the bottom, as having lived obliquely buried in the bottom, or as having been attached vertically by the apical end.

Ruedemann (1921) has shown conclusively that some of them were horizontal in their normal attitude. This is proved in the case of *Geisonoceras tenuitextum* of the Ordovician of New York by the preservation of a well marked longitudinal color pattern (Plate 4, fig. 5) on one side of the shell, which must have been the dorsal, since all marine organisms with a color pattern have the side toward the light contrasted with the opposite side. Not only so, but this author cites shells of this species with incrusting bryozoa in which the zoarium begins near the apex and extends forward on one side of the shell only, *pari passu* with its growth, which would be a most unlikely occurrence if the bryozoan had started on a dead shell.

If this dorso-ventral color pattern were an isolated case it might possibly be open to doubt, but it has been observed in specimens of orthocones of very different ages and widely separated geographically. Naturally the preservation of the color pattern of life in fossils of great antiquity is unusual, so that many such instances are not to be expected. Nevertheless I may cite such features in *Orthoceras trusitum* of the Silurian of New York, *Orthoceras anguliferum* of the Devonian of Germany (Plate 4, fig. 4), *Orthoceras* sp., of the Upper Carboniferous of Oklahoma, and I have no doubt that a protracted search through the systematic literature would disclose other instances. Those cited extend pretty well through the Paleozoic and over two continents, and I think that we may legitimately conclude that the horizontal attitude was the normal one for the majority of the orthocones.

Ruedemann considers such forms to have been benthonic and to have dragged their shells over the Paleozoic sea-bottoms. The objections to this interpretation are that their apertures are not oblique, the shells do not show wear incident to such a mode of life, and many show a hyponomic sinus which is usually correlated with a functional hyponomic funnel.

This last is not an especially weighty objection, since all cephalopods must have preserved the funnel for respiratory purposes even when it ceased to be functional as a locomotive organ; at least in the modern Nautilus its regular pulsation causes incurrent and excurrent streams, and the mantle does not take part in causing these movements, as it does in the dibranchiates.

I believe such forms to have been swimmers. Some doubtless hovered near the bottom or spent most of their time resting upon it, but others surely must have been more active. The idea that locomotion

backward was awkward is wholly anthropomorphic—it is to us, but is decidedly not for a cephalopod. The other idea that they would run the risk of fracturing the apex of the shell is altogether fanciful—they did not find their optimum conditions of life on a stern and rock-bound coast, and in any event nature usually provides against accidents in its tendency to overpopulation. (Pathological rostra of the Mesozoic belemnites are found fossil.)

Many students can not dismiss the idea from their minds that the cephalopod shells were too heavy and too unwieldy to have been propelled by the relatively simple method in vogue among these animals. This rests almost entirely upon the handling of museum specimens in which the chambers are filled with sediments, lithified, or calcified, or impregnated, or replaced with marcasite, etc. In the vast majority of forms throughout their whole geologic history, the shells were thin and in life were relatively light and easily propelled, and the specific gravity of the whole animal was close to that of the medium—so close, I imagine, that when the animal was expanded to its maximum extent it would float or rise in the water, and when withdrawn within its living chamber it would sink.

A belief in the swimming habits of the majority of orthoconic forms is also a reason for regarding them as having had "arms" like a squid rather than tentacles like a Nautilus, since when swimming these would trail behind, as do the extended tentacles in the Nautilus, and would furnish the necessary rudder to guide their passage through the water more effectively than tentacles. Obviously not all orthoconic forms were swimmers. I would expect such swimming forms to show some compression in the cross profile of the shell, and this is perhaps true in a majority of cases. Crawling or grovelling forms should show some depression in the cross profile of the shell, and this can be seen in a number of forms.

The extreme example of depressed shell form, undoubtedly indicating a sedentary bottom-dwelling animal, which had probably lost the swimming habit and could move only by dragging its shell by the use of its arms, is the genus *Gonioceras* (Hall, 1847). This includes five or six Ordovician species found in Ontario, New York, Illinois, Wisconsin, Minnesota, and northern China. The shell is several times as wide as it is high, with lateral flanges; the septa are closely spaced and sinuous; and the siphuncle is large and nummuloidal. At maturity the aperture is greatly constricted. Since the muscular attachment of the animal to its shell is not especially firm throughout the Cephalopoda, this constriction of the aperture in *Gonioceras* would serve to prevent the rupture of the muscular attachment when the shell was pulled along over the bottom, and the angularity of the septa would also serve to give the animal a firmer hold on its shell. Hyatt (1884 and 1900) made some wild guesses regarding the affinity of this curious form; we are not, however, at present concerned with its taxonomic position, but only with its obvious adaptation to a benthonic existence; from this point of view it is completely adapted, and ceases to be curious—the large nummuloidal siphuncle may be regarded as ballast, helpful in maintaining an even keel (Plate 2, fig. 17).

I have already mentioned the habit of some of the earlier orthocones of using the siphuncle in this way, or of filling the earlier chambers to a greater or less degree with organic deposits to counteract their buoyancy. Large and often elaborately ornamented siphuncles occur in a number of families of nautiloids, as for example in the families Endoceratidae, Pilo-

ceratidae, and Cyrtendoceratidae; and every degree of internal filling of the earlier chambers may be seen in the families Actinoceratidae, Jovellanidae, and Poterioceratidae—collectively covering the time from Ordovician to Devonian.

An equally effective method of maintaining horizontality is illustrated by the families Ascoceratidae and Mesoceratidae—constituting the sub-order Mixochoanites of Hyatt—Ordovician and Silurian nautiloids. In these the shells have advanced slightly beyond the orthoconic form in most of the genera and are more or less cyrtoconic. The living chamber of the adult is long and inflated, often contracted at the aperture, which is sometimes crested. The manner in which the center of gravity is kept back is by the formation of a linear series of air chambers (saddles) along the dorsal wall of the living chamber. Two examples of this are shown in the accompanying figures (Plate 3): *Proterocameroceras*—an orthoconic form, and *Ascoceras*—a cyrtoconic form. A somewhat similar arrangement is exhibited in the allied family Piloceratidae of the Ordovician. In *Piloceras* the shell is relatively short and wide; the animal was stout, its visceral cone extending backward over six-sevenths of the distance to the apex of the shell; the living chamber is restricted dorsally and the animal thus rendered buoyant by the development of numerous dorsal saddles (air chambers), and the apex of the shell is ballasted by pseudosepta and conchyolin endocones.

According to Geikie, (I have not taken the pains to verify his count) the Silurian of the Bohemian basin furnished Barrande with 1127 species of Cephalopoda. Of these 554 were orthocones, and other statistically minded students have estimated the number of orthocones in the Ordovician as approximately fifty per cent of the total number of species of Cephalopoda known from that period. The percentage is somewhat less for the Silurian as a whole, about 25 per cent for the Devonian, and about 20 per cent for the Carboniferous as a whole, although some very large sized forms do survive as late as Carboniferous times. In post Triassic times there are no orthoconic nautiloids. This proves that the general course of evolution in this sub-class was as I have indicated, and effectually combats the seemingly eccentric view of Owen—in which strangely enough he is followed by Willey and Spath—that the orthoconic are uncoiled from whorled ancestors.

THE CYRTOCONES

The number of species of cyrtocones in the Silurian of the Bohemian basin was 330. Both orthocones and cyrtocones were all originally referred to the two comprehensive genera *Orthoceras* and *Cyrtoceras*, but later systematists have partially segregated them into more natural generic groups. I have already indicated a probable variety of habits among the orthocones, and this is quite as clearly indicated among the cyrtocones. There can be slight doubt that what might be called the normal cyrtocone was derived from orthoconic ancestors in the manner already outlined, or that such a one as is shown in Plate 2, figure 5 was a horizontal swimmer.

Among the cyrtocones, however, there are a considerable number of so-called breviconic forms, all from the Silurian (Étage E), which it seems to me throw an important light on their structure and habits. They are all of about the same size, i.e. 4 to 5 centimeters long and 2 to 3.5 centimeters in maximum diameter, and hence justly called small forms, and are conspicuously marked by mostly transverse color patterns that entirely encircle the shell and prove conclusively

that these shells were held erect in life and equally illuminated on all sides. By the same token the animals were benthonic crawlers and not swimmers. Not only were they crawlers, but I believe that they crawled by means of a soled foot like that of a gastropod and not by means of their tentacles as does the existing octopus. In fact, were it not for their camerated shells and siphuncles one would be disposed to doubt their cephalopod character and consider them gastropods.

My restoration of *Cyrtoceras parvulum* Barrande will indicate sufficiently my conception of the animal (Plate 4). The extent to which the soled foot has assumed a tentacular form in front is, of course, entirely problematic. If these forms were organized as I have assumed, they would represent a survival, as late as the Silurian, through a continuous ancestry, of the primitive nautiloid organization of the early Cambrian or pre-Cambrian, and would be otherwise unrelated to their contemporary cyrtoceran associates.

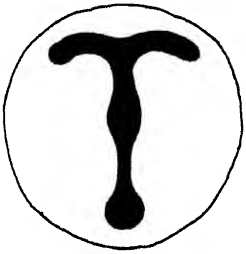
Among these cyrtocones with color patterns on all sides of the shell are *Cyrtoceras fallax* Barrande, with straight transverse bands; *Cyrtoceras zebra* Barrande, with closely spaced fine subparallel wavy bands; *Cyrtoceras intricans* Barrande, with somewhat more angular and less regular bands, more pointed backward than forward and perhaps prenuncial to chevrons; *Cyrtoceras veteranum* Barrande, with closely spaced chevrons; and *Cyrtoceras decurio* Barrande with large angular chevrons. A sixth species is ornamented with spots all around.

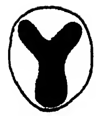
ADAPTATIONS FOR A MORE OR LESS PASSIVELY FLOATING MODE OF LIFE

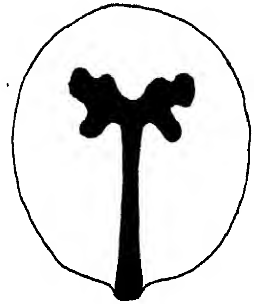
Adaptations by means of which the animal spent most of its existence in passively floating are various and are attained in unrelated stocks throughout the geological history of the class. Whether they floated near the surface, in intermediate depths, or hanging over the bottom—the feeding ground of the existing Nautilus—is immaterial; certainly those forms which retained locomotive powers could readily maintain their position at any desired depth. In the adaptation diagram (Plate 2) all floating forms have been placed near the surface, but this is solely a matter of composition on a crowded diagram. The recurved aperture in such an ammonite as *Macroscaphites*, or in some species of *Heteroceras* or *Nostoceras* leads to the conclusion that they drifted over the bottom while feeding, but in other genera there is no definite evidence on this point.

There are a considerable number of orthoconic Nautiloidea, prevailingly small and breviconic, found from the Ordovician to the Carboniferous, and principally in the families Rizoceratidae, Oncoceratidae, Poterioceratidae, and Trimeroceratidae, represented by a variety of genera, and exhibiting numerous differences in their structural details, which floated head downward by reason of the gas filled chambers of the apex of the cone. This type is illustrated in the diagram by *Mandaloceras* (Plate 2, fig. 15), a Silurian genus.

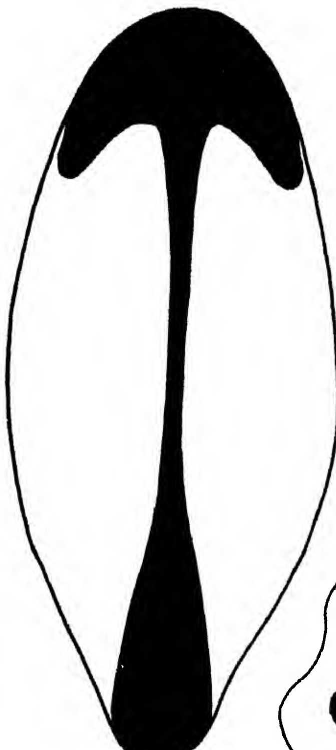
In *Mandaloceras* this position must have been maintained from infancy onward. At maturity the aperture of the living chamber was greatly contracted, but the hyponomic funnel probably retained its propulsive powers, since the space in front of it was not roofed over by the inflected margins of the aperture. The expulsion of water from the mantle cavity through the funnel would cause the animal to rise vertically. Many other of these forms had variously contracted apertures leaving only restricted openings for the eyes, tentacles, mouth, and funnel. Many students have thought that this was to be interpreted as indicating that their food

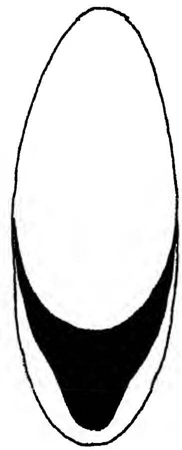

1

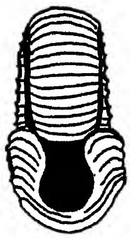

2

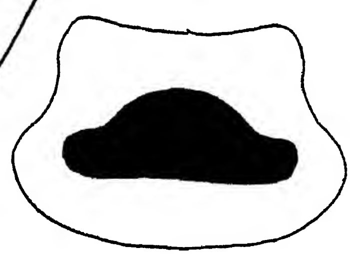

3


4


6

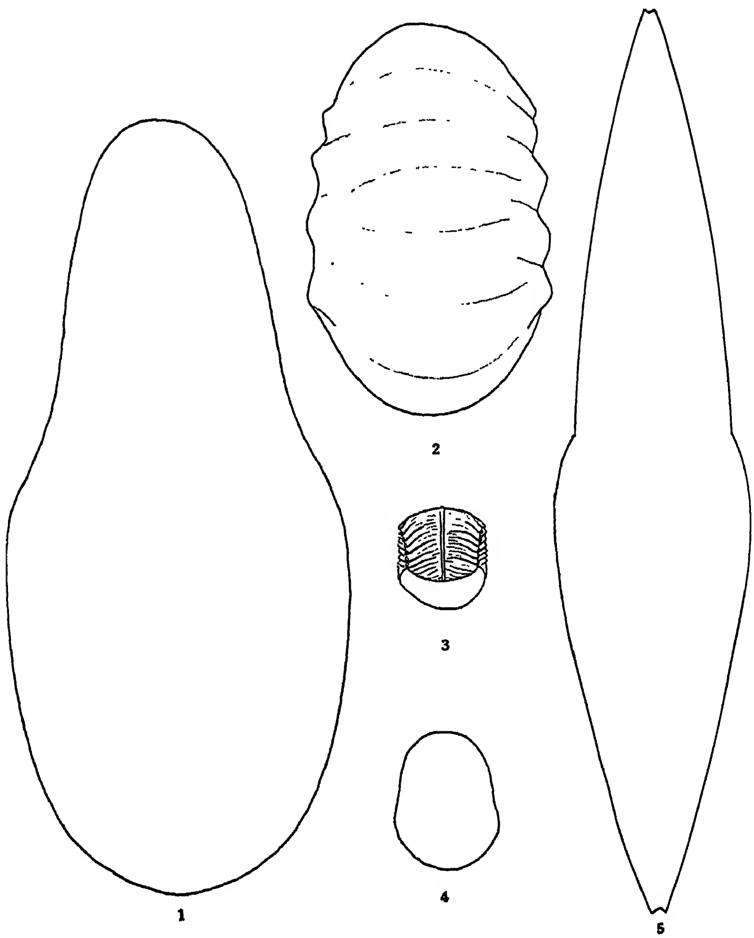

7


5


8

VIEWS OF VARIOUSLY CONSTRICTED APERTURES, ALL NATURAL SIZE

FIG. 1. *Mandaloceras bohemicum* (Barrande). Silurian of Bohemia.
FIG. 2. *Ophioceras simplex* Barrande. Silurian of Bohemia.
FIG. 3. *Tetrameroceras panderi* (Barrande). Silurian of Bohemia.
FIG. 4. *Morphoceras pseudoanceps* Douvillé. Bajocian of France.
FIG. 5. *Normannites braikenridgei* (Sowerby). Middle Jurassic of France.
FIG. 6. *Phragmoceras inflexum* Hedström. Silurian of Gotland.
FIG. 7. *Arcestes intuslabiatus* Mojs. Upper Triassic of Austria.
FIG. 8. *Hercoceras mirum* Barrande. Devonian of Bohemia.



END PROFILES OF VARIOUS CEPHALOPOD SHELLS, REDUCED ONE-HALF

FIG. 1. *Nautilus pompilius* Linné, the best known existing species of *Nautilus*
FIG. 2. *Polyptychites laticosta* von Koenen. Neocomian of Germany. (After von Koenen.)
FIG. 3. *Tropites subbullatus* (Hauer). Upper Triassic of Austria. (After Hauer.)
FIG. 4. *Cyclolobus stachei* Gemmellaro. Late Paleozoic of Sicily. (After Gemmellaro.)
FIG. 5. *Placenticeras meeki* Boehm. Upper Cretaceous of South Dakota.

was microscopic, and Abel has dubbed such forms microphagous. I see no reason for limiting the size of their food except by the size of the opening through which it had to pass (Plate 5).

The existing Nautilus is a voracious carnivore, very catholic in its taste. Doubtless the size of the aperture in such a fossil form as *Mandaloceras* imposed somewhat narrow limits with respect to size of the food particles, since it could not excert its jaws and tentacles through so narrow an opening and tear large sized prey to pieces. The contracted aperture was not, however, an adaptation due to feeding habits, but exactly the opposite, the contracted aperture having originated as a protective device which also served to keep the animal from becoming dislodged from its living chamber, exactly comparable with the apertures in such land snails as *Polygyra*, *Anastomia*, and *Pythia*. Such a form as *Mandaloceras*, if its aperture had been an open one, would have been a juicy morsel for its larger and more actively swimming contemporaries, and to call such apertures gerontic features is about as absurd as Schmidt's suggestion that the young may have been protected within the living chamber of the mother by them.

Many of these early floaters had shells which were cyrtocones, often endogastric, as in the Silurian nautiloid *Phragmoceras*, shown in the diagram (Plate 2, fig. 14). These were in general somewhat larger forms than the breviconic orthocones like *Mandaloceras*, but like them they retained the functional hyponomic funnel, and had greatly constricted apertures during their adult life. What was said of *Mandaloceras* applies also to forms like *Phragmoceras*, except that the latter could probably propel themselves horizontally. To rise or sink they would have to depend on the extension or contraction of the arms to induce changes in their specific gravity, unless, like the existing *Spirula*, they could point their funnel in different directions.

Another series of evolutionary changes in the direction of adaptations for floating is exhibited by those nautiloids whose ancestors had completely coiled shells (ophiocones). These may have open apertures, as in *Schroederoceras* (Plate 2, fig. 12), an Ordovician genus; or contracted apertures, as in *Ophioceras* (Plate 5, fig. 2), a Silurian genus. They are contrasted with such adaptations as *Mandaloceras* or *Phragmoceras* in that they were normal swimmers with normally coiled shells during adolescence. At maturity the living chamber became partially free (uncoiled), the margins being built outward to accommodate the growth of the animal, which was then strikingly elongated as compared with the short bodied *Mandaloceras* or *Phragmoceras*, and must have passed the remainder of its life suspended obliquely in the water—the weight of the body causing the shell to tilt forward.

The end product of such an evolutionary adaptation as *Ophioceras*, in which it is prenuncial, is exhibited by the nautiloid genus *Lituites* Breyn., which in early Paleozoic time (Ordovician) set an example of modification that was repeated in substantially the same way by ammonoid genera like *Macroscaphites*, eons later. *Lituites* was a fairly large form in which the first three whorls form an ophiocone, indicative of its ophioconic ancestry, as well as its normal swimming attitude during adolescence. After this stage of its ontogeny the diameter of the shell increases rapidly and it is nearly straight in its growth for a distance about 14 times the diameter of the coiled early portion. The aperture has a shallow hyponomic sinus, narrow ventro-lateral crests, broad

lateral sinuses, and fairly well developed dorso-lateral crests. The living chamber was extraordinarily long, and the consequent weight of the animal must have caused the shell to assume an almost vertical attitude in the water. The adult Lituites must have drifted, head down, picking up its food on or near the bottom. If the hyponomic funnel remained functional, as the presence of a hyponomic sinus would seem to indicate, it would serve to propel the animal upward, which would then sink slowly. A very slight action of the funnel would serve to keep the animal at any favorable horizon where food happened to be abundant.

Among the ammonoids floating adaptations are expressed in various ways. Least modified are various genera of the family Stephanoceratidae, such as *Normannites* Munier-Chalmas of the middle Jurassic, in which the aperture is so contracted (Plate 5, fig. 5) that it is difficult to visualize a functional hyponomic funnel, although this is not impossible. Another involutely coiled small form which seems to have been pelagic is the genus *Morphoceras* Douvillé (Plate 2, fig. 9) of the Jurassic and Cretaceous, in which the adult aperture was almost entirely closed and swimming would seem to have been precluded (Plate 5, fig. 4). I have pictured it as planktonic.

Modified in a different way are those forms which were tightly coiled in their youth, but which have the very long adult living chamber suspended, and frequently recurved near the aperture. A good example of this adaptation is furnished by the Lower Cretaceous genus *Macroscaphites* Meek (Plate 2, fig. 10), which, like the Ordovician nautiloid *Lituites*, must have been a swimmer in its youth. At maturity the body chamber hangs down for a distance about equal to the diameter of the coiled disk and finally curves upward at its lower end. I consider *Macroscaphites* to have normally drifted, foraging over the bottom, the position of the aperture raising the head above the bottom in an advantageous manner. Possibly the specific gravity was so adjusted that the shell would sink when the animal was withdrawn within the living chamber, and rise when it was extended; or when extended and foraging the funnel, by its action, might either reinforce the induced buoyancy or tilt the hook-shaped distal end of the shell so that the animal had no difficulty in seizing its prey on the bottom.

The genus *Hamites* Parkinson, of the Cretaceous, functioned exactly as did *Macroscaphites*, only in the former genus the early shell was not tightly coiled but was a gyrocone. All of the members of the sub-family Scaphitinae, as exemplified by the genus *Scaphites* Parkinson, a world-wide Cretaceous type, were more or less floaters. Indeed it is difficult to see how the adult of such a species as the Cenomanian *Scaphites aequalis* Sowerby could have swum at all. On the other hand it is readily conceivable that a form with the aperture oriented as in *Scaphites spiniger* Schluter—a German Upper Cretaceous species—might well have been able to swim.

Still another type is illustrated by such genera as *Spiroceras* Quenstedt of the Jurassic (Plate 2, fig. 21), or *Crioceras* Leveillé and *Ancyloceras* d'Orbigny, of the Cretaceous. In these the shell is a gyrocone, and such a type might well be a form leading in the direction of *Hamites* (supra). Another form that appears to me to indicate a floating existence is such a species of *Heteroceras* as *Heteroceras reussianum* d'Orbigny (Plate 2, fig. 22) from the Upper Cretaceous of Germany. This was relatively a small form with a

shell coiled in an open ascending spiral, its apertural end recurved as in *Macroscaphites*, and, I believe, had from infancy the habits described above for the mature Macroscaphites. The genus *Heteroceras* of d'Orbigny is confined to the Cretaceous period, and all of its species have trochoid spiral shells, but many tend to irregularity, and some appear to have been benthonic crawlers rather than pelagic. Such a form as *Heteroceras stevensoni* appears to me to have had a crawling rather than a swimming or floating habit.

Such genera as *Hamulina* d'Orbigny and *Ptychoceras* d'Orbigny of the older Cretaceous appear to include highly anomalous forms. During growth their shells are relatively slender chambered orthocones, and if the earlier chambers contained gas, as there are no reasons for doubting, it is impossible to see how they could have been oriented except head downward. At maturity the shell, now much enlarged, bends through an arc of 180 degrees and continues its growth in the opposite direction, the animal now facing the apex of the shell. This adult enlargement of the body, faced about as it was, would thus shift the center of gravity backward, so that the animal would now be able to swim in a horizontal position, as I have indicated (Plate 2, fig. 26). In some species of *Ptychoceras* the living chamber extends further backward than in the species that I have figured. For example, in the much smaller Neocomian species, *Ptychoceras emericianus* d'Orbigny, it extends three-fourths of the distance toward the apex of the shell.

In the genus *Ptychoceras* the flexed portion is in contact with the earlier part of the shell. *Hamulina* differs merely in that the two parts do not come into juxtaposition. Hyatt and other authors speak of such forms as these partially uncoiled or secondarily straightened ammonites as "degenerate," but they are obviously not degenerate in any way unless one adopts a creed, and considers the closely coiled form of shell the ideal of perfection. Doubtless the last was an ideal for a swimming habit, and that is why such forms predominate in the geological record of the Mesozoic era, but from the point of view of adaptation a Macroscaphites was more specialized, and in its adult form would have avoided a certain amount of competition which it suffered in its youth. If cephalopods, or other organisms, can have imputed to them any purposes other than to live and reproduce their kind, then, and then only, is it permissible to speak of modifications such as these as degenerate.

ADAPTATIONS FOR A CRAWLING BENTHONIC LIFE

In considering the mode of life of the swarming ammonites of the Mesozoic and in endeavoring to find some sort of seemingly rational explanation for their remarkably complicated septa, the older naturalists, noting that the growth lines across the venter and the margin of the aperture, when this was preserved, usually showed no trace of a hyponomic sinus such as is present in the majority of the nautiloids, reasoned that there was no hyponomic funnel, and hence that the ammonites as a group were not swimmers, but crawlers on the bottom by means of their tentacles; and that this habit had induced the development of the lobes and saddles in the septa, since this would enable the animal to hold and balance its shell more effectively while crawling.

This view has been widely accepted, although it is open to insuperable objections. It entirely ignores the meaning of their prevailingly high and often greatly compressed, bilaterally symmetrical, planospiral shells; it ignores the fact that

a hyponomic funnel is essential for respiration; it ignores the universal principle of organisms, namely: that a dominant group tends to utilize all available habitats more or less completely; and it disregards the meaning of the wide geographic range that a number of species show.

Narrow planospiral shells fulfil what might be called the stream-line form for disks. Many, such for example as a large Sphenodiscus, have lines that obviously indicate a movement through the water, and how such high and narrow shells could have been manipulated by a crawling animal is incomprehensible. It is true that there are a number of genera of benthonic gastropods scattered through many families and sub-orders that have planospiral shells. In the planospiral gastropods the shells are generally small and their apertures wide—usually wider than high. None approach the cephalopod shell-form, unless it is the tiny early stage of the genus *Caecum*, so that I think it may be conceded that the normally lenticular form of the coiled Cephalopoda —whether nautiloids or ammonoids—is indicative of a swimming habit.

There are, however, great differences in the transverse profiles of their shells, which doubtless indicate different degrees of resistance to slipping through the water, and in a general way ammonites as a whole are more compressed than nautiloids, the most compressed ammonites, with "cut water" keels or venters, being, in general, among the later forms.

Among the coiled shells of both nautiloids and ammonoids the swimming ability was not only conditioned by the form of the shell and the resistance it offered to passage through the water, but also by the power of the hyponomic funnel, and there is no means of obtaining information on this second factor, since I do not regard the presence or absence of a hyponomic sinus as a reliable indication. This last may perhaps be used with caution, but there are forms—*Placenticeras*, for example—that I regard as active swimmers, but that show no hyponomic sinus.

Transverse profiles of various forms from all horizons show variations from wide ellipticity to extreme compression. The existing Nautilus, which has almost as blunt prowed a shell as can be imagined (Plate 6, fig. 1), a shell certainly wider than in the majority of fossil forms, is known by observation to swim moderately well, which shows how cautiously shell form must be used in predicating locomotive ability. I have shown three more depressed and wider forms in the accompanying illustrations—a *Polyptychites* (Plate 6, fig. 2) from the Lower Cretaceous, a *Tropites* (Plate 6, fig. 3) from the Triassic, and a *Cyclolobus* (Plate 6, fig. 4) from the late Paleozoic, all of which would seem to have been exceedingly poor swimmers. For comparison with these a profile of *Placenticeras*, with what I regard as fast lines, is shown. I believe that all highly compressed forms, and the ammonites show them at all later horizons—*Sageceras* and *Pinacoceras* (*layeri* Hauer) from the Triassic, *Oxynoticeras* from the Jurassic, *Placenticeras* and *Spenodiscus* from the Upper Cretaceous, etc.—were rapid swimmers. Otherwise their shell form is meaningless, and it is impossible to imagine the animal as having been able to handle such high and narrow shells in any other way.

There are shell forms, however, both among Nautiloids and more commonly among the Ammonoids, appearing sporadically throughout all cephalopod history from the Devonian to the Upper Cretaceous, that became secondarily adapted for a benthonic mode of life. All trochoid

shells, unless they can be referred to habits of life such as I inferred for *Heteroceras reussianum* (supra), may be considered to have led a benthonic existence, and their shells, although much less diversified, may legitimately be compared with those exceedingly numerous gastropods whose shell plan is an ascending spiral. Instances of a greater degree of reversed adaptation are furnished by the marine limpet-like pulmonates *Siphonaria* and *Gadinia*, whose ancestors became terrestrial, their descendants of these two genera reentering the sea and becoming benthonic.

That such modifications of the cephalopod shell are not confined to the closing days of ammonite history, but occur also in the Paleozoic nautiloids, is proof that they are adaptations, and not degenerations or phylogerontic features. As I have stated, trochoid shells are far more numerous among ammonoids than among nautiloids; and among the latter are unknown from horizons earlier than the Devonian. This is just what might be expected if cephalopod evolution was anything like I have outlined. Not only did they take their origin from a benthonic stock, but it required long ages to acquire the coiled shell. Even as late as the Devonian 25 per cent of the cephalopods were orthocones and, as has been shown, some of these were benthonic, as were also the breviconic cyrtocones, so that there was no especially untilled field on the sea bottom to tempt the adoption of this mode of life among the nautiloids.

We may also infer from the transverse profiles of the shells, although this is highly problematic, that the nautiloid swimmers as a class were less effective swimmers than the later ammonoids, and fed for the most part near the bottom, as does the existing Nautilus. We may also infer that competition for food was keener among the Mesozoic ammonoids than it was among the Paleozoic nautiloids, or that the food of the latter was more exclusively nectonic, so that there would have been a greater stimulus for the adoption of a benthonic habit in the Mesozoic than in the Paleozoic, although this is very hypothetical. Nor can the influence of the great abundance of mostly benthonic arthropods in the older Paleozoic (trilobites and meristomes), or of the arthrodiran, ostracoderm, and true fishes, be ignored in seeking an evaluation; but the influence of these factors, important as they are, is so obscure that I will not attempt to discuss them.

A secondarily benthonic nautiloid, descended from a coiled swimming ancestor is the Devonian genus *Trochoceras* Barrande. Among the ammonoids the small Cochloceratinae, as exemplified by such genera as *Cochloceras* Hauer, or *Paracochloceras* Mojs., of the marine Triassic, may be mentioned as among the earliest. In the later Mesozoic there are a number of such genera, for example: *Turrilites* Lamarck, *Emperoceras* Hyatt, *Helicoceras* d'Orbigny, and probably some species of *Heteroceras* d'Orbigny—all from rocks of Cretaceous age. The first especially often reaches a large size. Two of these secondarily benthonic ammonoids are shown in the adaptation diagram (Plate 2, figs. 19 and 20). Doubtless the empty early chambers in these forms so reduced their specific gravity that the energy of handling them was reduced to a minimum.

The extreme of benthonic adaptation is that of the apparently sessile, or at least static, genus *Nipponites*, described by Yabe recently from the Upper Cretaceous of Japan, but much fuller information is desirable before attempting to visualize its habits. *Nipponites* was irregularly coiled like some species of *Vermetus* or *Serpula*—a tendency which may be said to

be shown to a very slight degree in species of *Heteroceras* or *Nostoceras*, but which in its extreme development in *Nipponites* is, for the present, highly anomalous. As in the Gastropod genus *Vermetus*, *Nipponites* was undoubtedly derived from a trochoid coiled ancestor.

THE PROBLEM OF SEPTA AND SUTURES

The familiar septal and resulting sutural progression from nautiloid (smooth curves), through goniatitic (angular) and ceratitic (frilled lobes), to ammonitic (frilled or digitate lobes and saddles), is well known, and in a general way is an epitome of the evolution of these parts. It is not, however, a simple linear series. Early forms often show unusual specialization, and later forms simplification, but it is well to avoid the philosophic implications of the terms acceleration and retardation, so much a part of the vocabulary of the cephalopod students of the penultimate generation.

A comparable change from septal simplicity to septal complexity may be observed in the ontogeny of the more evolved types, and this is the basis for the enormous literature on the biogenetic law as exemplified by the shelled cephalopods. It is commonly assumed that the sutural are the most constant features, and that however much the body-form or ornamentation may vary, the court of last resort in determining genetic relationships is the suture, which is said to be constant in species when individuals of the same degree of maturity are compared. This has now become a tradition among students of ammonites, but like all similar traditions, it is unsound, and the only way to establish it would be for systematists to consider every slight variation indicative of distinct species. In an account, shortly to be published, of the ammonite faunas of Peru, a student of mine, M. M. Knechtel, has shown considerable variation of single sutures on the two sides of the shell, and similar features have occasionally been recorded by earlier workers. In such a case the dogmatist must either admit sutural variation or contend that the two halves of the same shell belong to different species.

It is not my purpose in this essay to go deeply into this vexed question, with all its implications, but it may be stated as a general principle that the taxonomic value of such features as sutural pattern, shell form, ornamentation, etc., will vary greatly from genus to genus. In some cases one and in other cases another feature will be entitled to the greatest weight, but there will be no single magical criterion.

The factors that led to the increasing complexity of septa in the ammonoids have been a favorite field for speculation since von Buch first emphasized its existence by proposing the so-called genera *Goniatites*, *Ceratites*, and *Ammonites*. The subject remains obscure to the present, and none of the suggestions that I have encountered seem satisfactory. That it is related in some way to habit would seem probable by the essentially goniatitic form of the sutures in such a nautiloid as *Aturia*, which every beginner thinks is an ammonite; but that benthonic forms can be distinguished from planktonic or nectonic by the characters of the sutures, as Schmidt implies in a recent paper, or that Keferstein's wholly hypothetical "pre-septal gas" shows that animals with highly complicated sutures were divers, is wholly without foundation.

In a way progressive sutural complexity is to be correlated with increase in bodily size in excess of increase in shell capacity. This is also a factor in the corresponding sutural modification during ontogeny, for

I do not believe that all of the blame can be fastened upon the hereditary genes. Also, and more clearly, it is to be correlated with a more secure connection between the animal and its shell. This is to be rather conclusively inferred from the complementary relationship between the degree of development of adjacent lobes and saddles, where highly modified laterals tend to bring about underdevelopment in their fellows.

We are now fairly familiar with the formation of the septa in the existing Nautilus, which have their inception in the epidermis of the hind part of the visceral sac; this first becomes a membrane, is then conchyolinized, and finally calcified from the periphery inward on its anterior side next the animal. Hence the horny nidus is left behind the calcified septum. That septa are formed periodically, and alternately with periods of active metabolism, is inferred from their general regularity of spacing and from the correlation between growth lines of the shell and the spacing of the septa, as is shown, for instance, in Ruedemann's description of the shell of an Ordovician species of *Geisonoceras*.

It was long supposed that the flaccidity following the expulsion of the sexual products marked the time of septal formation, but as Willey has shown in *Nautilus*—and I think that his observation may be used for generalization—the last septum is formed before puberty. Perhaps septal formation may be correlated with seasonal climatic change, either as a direct factor or through the influence of climatic change upon food supply, although it must be admitted that seasonal climatic variations are minimized in the seas.

If snakes had shells, the annually shed skins would be accumulated in such a shell exactly (homologously) as are the endocones of the early Endoceratidae, and we may visualize in this periodic shedding of the hardened skin of the apical cone in the earliest nautiloids the beginnings of septal formation. If the extinct cephalopods had some muscular connection between the hinder part of the body and the shell in the region where the septum joins the shell wall, such a connection would supplement the comparatively feeble attachment of the lateral and annular muscles, and would influence the crumpling of the apex of the visceral cone; or, if there was such a connection directly between the body and the septum, any increase in the area of the latter by folding would increase the effectiveness of such a union; or, not to go beyond the well ascertained facts of observation, such a folding of the septum around its periphery—whether of a goniatitic or ammonitic character—into which the periphery of the hinder mantle penetrated, would enormously strengthen the bond between the animal and its shell, even though they merely remained in juxtaposition and were not directly united.

LIST OF LITERATURE

Abel, O. Paläobiologie. 1912.

Barrande, J. Système Silurien de la Bohème. Vol. 2. Céphalopodes. Prague, 1867–1877.

Benecke, E. W. Lebensweise der Ammoniten. Abh. Spezialkarte Elsass-Lothringen, N. F., Heft 6, 1905.

Branco, W. Beiträge zur Entwickelungsgeschichte der fossilen Cephalopoden. Palaeont., Bd. 26–27, 1880–1881.

Bubnoff, S. von. Über die Lebensweise und das Aussterben der Ammoniten. Naturwissenschaften, Heft 32, 1922.

Buckland, W. Notiz über die hydraulische Wirkung des Siphos bei den Nautilen, Ammoniten u. a. Polythalamien. Neues Jahrb., 1835.

Buckman, S. S. Type Ammonites. Vols. 1–5, 1909–1926.

Chun, C. *Spirula australis* Lam. Ber. Math.-phys. Kl. Sächs. Gesell. Wiss., Bd. 62, 1910.

———. Valdivia-Expedition, Cephalopoden. Bd. 18, 1910.

Crick, G. C. Muscular attachment of the animal to its shell in Ammonoidea. Trans. Linn. Soc., ser. 2, vol. 7, 1898.

Dean, Bashford. Notes on living Nautilus. Amer. Nat., vol. 35, 1901.

Diener, C. A critical phase in the history of Ammonites. Am. Jour. Sci., vol. 4, Aug. 1922.

Diener, K. Lebensweise und Verbreitung der Ammoniten. Neues Jahrb. Beil., Bd. 2, 1912.

Dollo, L. Les céphalopodes déroulés et l'irréversibilité de l'évolution. 1922.

Douvillé, H. Note sur l'*Ammonites pseudo-anceps* et sur la forme de son ouverture. Bull. Soc. Geol. France (III), tome 8, 1880.

Douvillé, R. Influence de la mode de vie sur la ligne suturale des ammonites appartenant à la famille des Cosmoceratides. Compt. Rend. Acad. Sci., tome 156, 1913.

Dunbar, C. O. Phases of cephalopod adaptation. Chapter VI of Organic Adaptation to Environment. 1924.

Foord, A. H. Catalogue of the Fossil Cephalopoda in the British Museum. Pts. 1–3, 1888–1897.

Frech, F. Losses und geschlossenes Gehäuse der tetrabranchiaten Cephalopoden. Centralblatt f. Min. Geol. & Pal., 1915.

Griffin, L. E. The anatomy of *Nautilus pompilius*. Mem. Natl. Acad. Sci., vol. 8, 1900.

Hall, James. Palaeontology of New York, vol. 1, 1847.

Hedström, H. Ueber die Gattung Phragmoceras in der Obersilurformation Gotlands. Sver. Geol. Unders., Ser. Ca, No. 15, 1917.

Hoernes, R. Zur Ontogenie und Phylogenie der Cephalopoden. Jahrb. Geol. Reichsanst., Bd. 53, 1903.

Holm, G. Ueber die innere Organisation einiger silurischer Cephalopoden. Palaeont. Abh., Bd. 3, 1885.

———. On the apical end of Endoceras. Geol. Fören. Förhandl., Vol. 18, 1896.

Hyatt, A. Genera of Fossil Cephalopods. Boston Soc. Nat. Hist. Proc., vol. 22, (1883) 1884.

———. The phylogeny of an acquired characteristic. Proc. Am. Phil. Soc., vol. 32, no. 143, 1894.

———. Cephalopoda in Eastman-Zittel. 1900.

Hyatt, Alpheus and Smith, J. P. The Triassic cephalopod genera of America. U. S. Geol. Survey Prof. Paper 40, 1905.

Jaekel, O. Thesen über die Organisation und Lebensweise ausgestorbener Cephalopoden. Zeit. Deutsch. Geol. Gesell., Bd. 54, 1902.

———. Neue Beobachtungen an Orthoceren. Juni-Protokoll Deutsch. Geol. Gesell., Jahrg. 1903.

Naef, A. Über Bau und Lebensweise der tetrabranchiaten Cephalopoden. Vierteljahrischesschrift Naturf. Gesell. Zürich, 66. 1921.

d'Orbigny, C. Paléontologie française. Terrain crétacé I. Céphalopodes, 1840. Terrain jurassique, Céphalopodes, 1852.

Owen, R. Memoir on the Pearly Nautilus. London, 1832.

Perna, E. Ueber die Lebensweise der Goniatiten. Geol. Wiestnik, St. Petersburg, 1, No. 1, 1915.

Pfaff, E. Über Form und Bau der Ammonitensepten und ihre Beziehungen zur Suturlinie. 4. Jahresber. Niedersächs. Geol. Verein, 1911.

Pompeckj, J. F. Paläontologie. Cephalopoda. Handwörterbuch d. Naturwiss., Bd. 2, 1912.

Ruedemann, R. Structure of some primitive cephalopods. Rept. N. Y. State Paleontologist, 1904.

———. Observations on the mode of life of primitive cephalopods. Bull. Geol. Soc. Amer., vol. 32, 1921.

———. On sex distinctions in fossil cephalopods. On color bands in Orthoceras. 16th Rept. Director State Museum N. Y., 1921.

Schmidt, J. Live specimens of Spirula. Nature, vol. 110, pp. 788–790, 1922.

Schmidt, Martin. Ammonitenstudien. Siergel's Fortschritte der Geol. und Palaeont., Heft 10, 1925.

Smith, J. P. The Carboniferous ammonoids of America. U. S. Geol. Surv. Mon. 42, 1903.

———. Acceleration of development in fossil cephalopoda. Leland Stanford Junior Publ., 1914.

Solger, F. Die Lebensweise der Ammoniten. Naturwiss. Wochenschrift, N. F. 1, 8, 1901.

Steinmann, G. Beiträge zur Stammesgeschichte der Cephalopoden. Zeits. f. induktive Abstammungs-und Vererbungslehre, Bd. 36, Heft 3/4, 1925.

Trueman, A. E. Aspects of ontogeny in the study of ammonite evolution. Jour. Geol., vol. 30, 1922.

Tschernov, A. Les traits fondamentaux de l'évolution des ammonites. Bull. Soc. Nat. Moscou, tome 31, 1922.

Willey, A. Contribution to the natural history of the pearly nautilus. Zoological Results, vol. 6, 1902.

THE LIFE CYCLE AND MATING HABITS OF THE MALE TARANTULA

By W. J. BAERG

University of Arkansas

(Research Paper No. 78, Journal Series, University of Arkansas)

THE tarantula, *Eurypelma californica* ausserer, is very common in a number of our southwestern states, such as California, Arizona, New Mexico, Texas, Oklahoma, Arkansas, and probably others. In Arkansas it occurs in smaller or greater colonies in various regions where conditions with reference to shelter and food are favorable. Hillsides in meadows, or woodland not completely shaded, that are relatively free from weeds and tall grass, may be regarded as suitable ground, especially if numerous flat rocks of medium size are available for shelter. Although the spiders can and do dig their holes, they very frequently do no more than dig an entrance underneath a large flat rock, where they may live for several years.

A colony of from twelve to fifteen spiders is located near the university campus, and has been under fairly close observation for nearly nine years. For more intensive study, a varying number of tarantulas have been kept in the laboratory where they are placed singly in large battery jars, provided with an inch or two of soil and a dish with water. The jars are covered with screen wire tops. If the spiders are kept in a cold room, they will not require any food from early in October till late in March. During the rest of the year, they are fed on live grasshoppers, cockroaches, caterpillars, and some other insects. A full grown tarantula will require no more than one large grasshopper, such as *Melanoplus differentialis*, every five or six days. The small tarantulas, up to two-and-a-half years old, are fed on termites.

The sexes in mature tarantulas are readily distinguished by the fact that the males have longer legs in comparison with the size of the body, and by the relatively short and somewhat club-shaped palpi.

In the field observations the males have till recently been very puzzling. In spite of much diligent searching in many places, I have never seen a male out of doors except during the mating season. (In the Canal Zone, I have seen the males at night sitting presumably in front of their own holes, just as the females were doing. This was in August. Whether it was the mating season, I cannot say.) At this time the males may be seen sitting near the holes occupied by females, or wandering about in the neighborhood of these holes. The mating season extends through most of the months of September and October. All the males that have been brought into the laboratory died soon after the mating season was over, usually during the month of November. One male lived through the winter and till the following July.

This account of the life cycle is based

on observations made on a number of spiders in various stages of development, ranging from newly hatched individuals to fully matured adults. No individuals have been under observation throughout their life time from hatching till death after maturity; but the observations that have been made for a number of years on

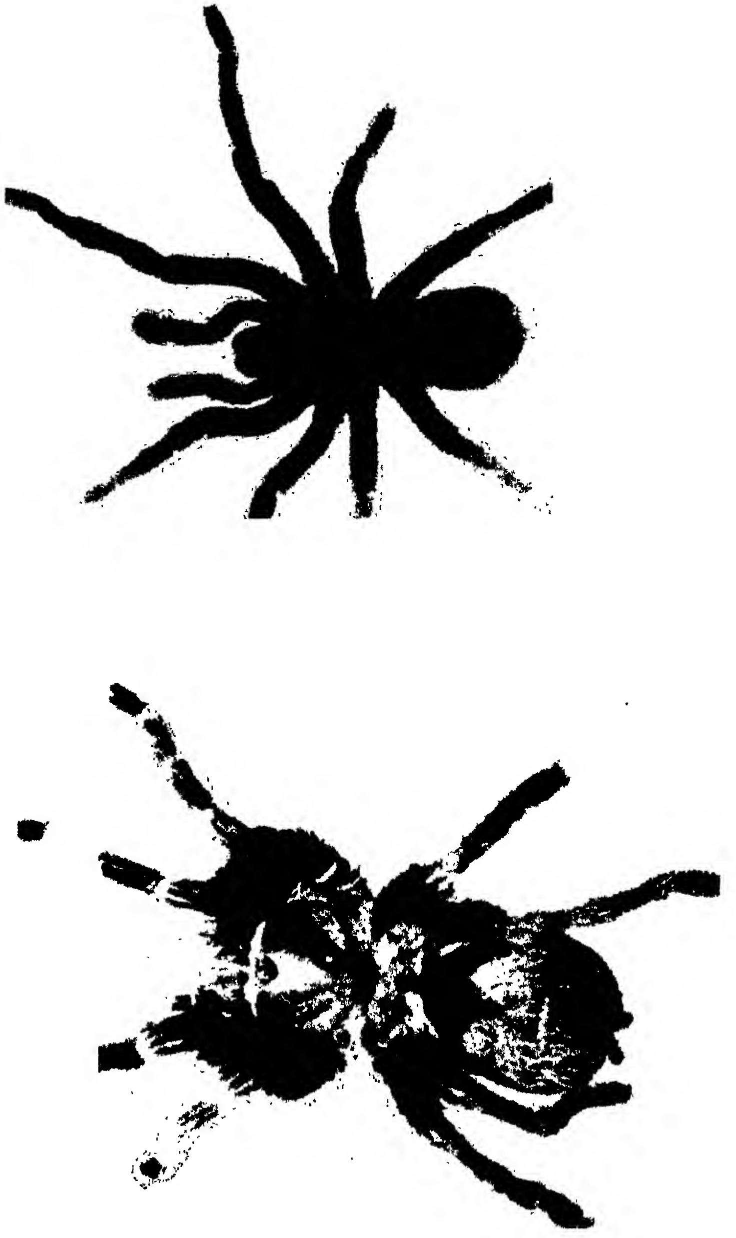


FIG. 1. ABOVE: MATURE MALE TARANTULA. BELOW: FEMALE TARANTULA 14 TO 16 YEARS OLD
(Photograph by David G. Hall)

spiders of various sizes will probably serve to make out a reliable account of the entire life cycle.

GROWTH

Measuring the total length of the spider at certain intervals of time is obviously not a very exact way of observing the growth; for the abdomen may vary in size between fairly wide limits. The increase in the length of the carapace is perhaps a more reliable indication of the growth; but since the records of this have been kept for only a few years, they are not suitable for use here.

The rate of growth of tarantulas from the time of hatching until the age of three-and-a-half years has been observed (see accompanying table), as has that of somewhat older tarantulas of various sizes. By putting these figures together, a table has been constructed which represents with a fair degree of accuracy the annual growth throughout the entire life cycle of a male tarantula.

Regarding the estimate of the ages of the various spiders represented in the table, some explanation is perhaps desirable. Although WF, when first measured, was 18 mm. long and but slightly longer than McI_6 at the age of three-and-a-half years, the former has been estimated at a year older, for the reason that conditions in the laboratory are more favorable than those out of doors. The unusual growth that it made during its first year and a half in the laboratory lends support to this assumption. At the age of eight-and-a-half years it measured 37.4 mm. RT_1 when first measured was 37.5 mm., and therefore fitted well into the age of eight-and-a-half years. This male reached maturity last fall (1927) at an estimated age of eleven years. There is a possibility that his age was one year less than that, but it is more likely that he was older, perhaps twelve years.

The tarantulas probably do practically all their hunting right in front of their holes, where they patiently wait night after night for a suitable beetle, cricket, or other insect. They locate their prey wholly by the sense of touch. Thus a cricket may come within a centimeter of where the tarantula is waiting, and be perfectly safe; however, as soon as one touches the other, the cricket is very speedily brought in reach of the fangs and consumed. From this method of hunting, it seems obvious that the tarantulas must often undergo longer or shorter periods of fasting. And from observations in the laboratory, it appears that Nature has equipped them well for this; for they can easily go without food for a month or six weeks and probably longer. As a result of the fasting, the time required

Annual Increase in Size

(In millimeters)

	½ YEAR	1½ YEARS	2½ YEARS	3½ YEARS	4½ YEARS	6 YEARS	6½ YEARS	7½ YEARS	8½ YEARS	9½ YEARS	10½ YEARS	11½ YEARS
WH_2	6.8	10.8	16.6									
McI_6		10.0	13.3	17.6								
WF					18.0	28.0	32.5	35.2	37.4			
RT_1									37.5	46.4	48.5	47.3

Measurements were made during the winter, from the last week in December till the first week in February, except the 6-year record, which was taken in the following July.

for reaching maturity will probably vary by as much as two years.

If the observations made on the several spiders may further be applied to RT_1, the mature male, he has gone through the following molts: the first molt about three or four weeks after hatching, when emerging from the cocoon; four molts in the following year; two molts in each of the next seven years; and one in each of the last three years, making a total of twenty-two molts for the entire life cycle.

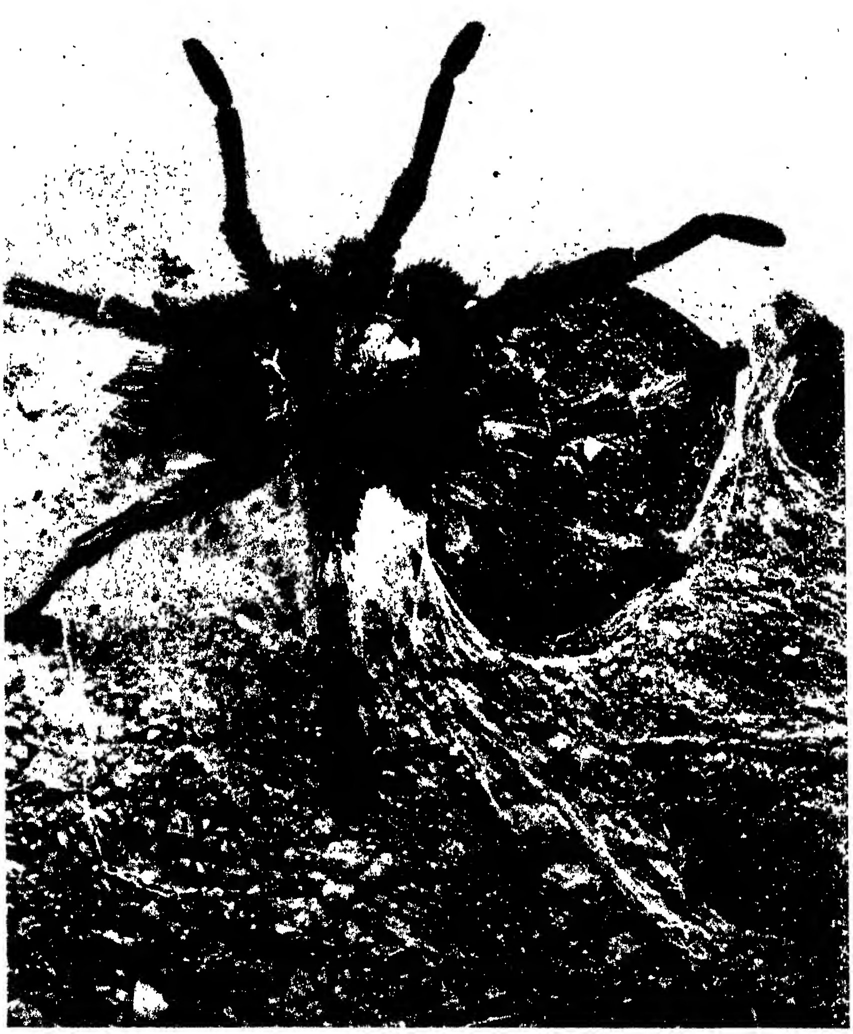


FIG. 2. MALE TARANTULA OVER SPERM WEB
(Photograph by W. J. Baerg)

During the four years that RT_1 has been under observation, he was taken for a female. The legs apparently resembled,

in proportion to the body, those of the female, and the palpi were relatively long and slender like those of a female. When he went through the last molt he emerged from the old skin, a mature and fully equipped male. The suddenness with which he changed from the state of adolescence to ripe manhood is striking. His transformation, coupled with the fact, already mentioned, that all the males brought into the laboratory died soon after the mating season, explains why adult males are never seen out of doors except at mating time.

MAKING THE SPERM WEB

After attaining maturity the male is not slow to realize Nature's purpose in his life. On the sixth day after the last molt (August 28), he made his first sperm web and presumably charged his palpal organs. Ten days later (September 7), a second web was made; five days later a third (September 12); and eighteen days later (September 30), a fourth. This last web was made twenty-four hours after he had mated with one of the females in the laboratory. The making of this fourth web, his last one, I was able to observe.

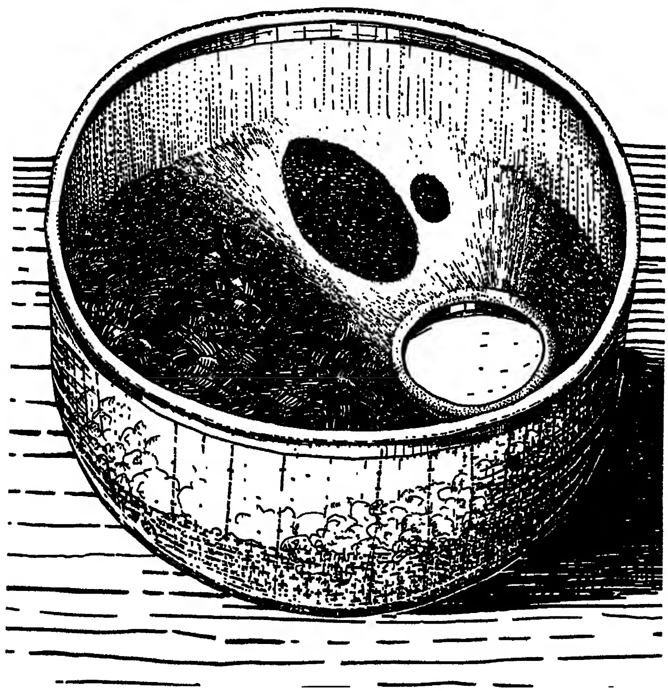


FIG. 3. SPERM WEB IN BATTERY JAR
(Drawing by David G. Hall)

The web was made in a battery jar nine inches in diameter. On one side the web was fastened to the soil at the bottom, and on the other side on the wall of the jar. The male began weaving at 9:20 a.m. As his abdomen swung right and left, the spinnerets moved gracefully up and down, touching here and there to fasten the threads. With the hind legs, he felt for the proper place of attachment of

threads, determined where the web needed to be strengthened, and outlined in a general way the two openings. This weaving was done while the male stood over the web, and was finished in forty minutes. The male now turned around several times while examining and reinforcing the web, and then facing towards the large opening and putting the first two pair of legs forward, he moved forward and turning over on his back slid easily through the large hole, under the web. Thereupon he turned around, remaining on his back but facing again towards the large opening.

After resting for about one minute, he proceeded with the second stage in the construction. This is done while the male is on his back, and is mainly the strengthening of the margin around the small oval opening, and in particular the narrow band between this opening and the large one. This band when finished is quite thick, and densely woven, much more so than the rest of the web. This stage of the construction was finished in fifteen minutes, and the web was completed.

Then the male brought the ventral surface of the abdomen up against the web, so that the margin of the genital opening was in contact with the narrow band between the two openings in the web. By moving the abdomen from side to side and pressing against the band, he rubbed the margin of the genital opening for a period of twenty minutes. During this time he was also stroking the genital bulbs. The fangs were partly opened and the bulbs were drawn through between the fang and the row of teeth. This process seemed very thorough and elaborate. The hair near the fangs appeared rather shiny, but careful examination through a binocular lupe failed to show any moisture. From time to time in this stroking process the fangs would open wider than usual and gently clasp the distal portion or tarsus of the palpus.

The process of rubbing the margin of the genital opening (doubtless for the purpose of stimulating the sex glands) and stroking of the genital bulbs continued for fifteen to twenty minutes. Then the droplet of spermatic fluid appeared in the genital opening and was deposited on the under side of the narrow band. Thereupon the male speedily came out from under the web, got on his feet, turned around and proceeded at once with the tapping or charging of the genital bulbs. Sitting over the web so that his cephalothorax projected partly over the smaller opening, he tapped with the tips of the bulbs alternately in the drop of spermatic fluid on the under side of the narrow band. At first the tapping was slightly irregular, but soon it proceeded with an almost machine-like regularity, each palpus beating at the rate of 135 to 150 taps a minute.

The charging of the genital bulbs occupied the male for an hour and forty-five minutes. Towards the end of the process, he tapped a bit slower, then walked around a bit, tapping here and there as if to make sure that all the fluid had been taken up. Then he seized the web with both fangs, pulled backward, and stooping down to get a better hold on the web, he walked forward and took practically all of it with him. After tapping the ground a few times with his palpi he settled down to rest. Later in the afternoon, I placed a female in the jar with the male, but he was not in the mood for mating. On the afternoon of the following day, this was tried again and mating took place.

MATING

The mating process of *Dugesiella hentzi* has been very fully described by Dr. Alexander Petrunkevitch of Yale. Dr. Vital Brazil gives a brief description of the mating of *Gramnostola longimana* and *G. acteon*. Among the higher spiders, the mating of the house spider has been carefully observed and described by Dr. H. E. Ewing of the U. S. National Museum. Wilhelm Bölsche gives a vivid account of the mating habits of *Araneus diadematus* (*Epeira diademata*), a European species.

It is relatively easy to observe the mating of tarantulas. If a male is brought in during the mating season and put with a female, mating is likely to take place provided the male has provided the bulbs with spermatic fluid. If not, he may be kept a few days until this has been done. The females will mate several times, as Dr. Petrunkevitch has observed in *D. hentzi*. One female mated thirteen times with four different males.

Mating in *Eurypelma californica* has been observed ten or twelve times. The male to whom this account is largely devoted mated twice with the same female. My notes of his first mating will perhaps serve to describe what usually takes place:

When the male was placed in the jar with the female she at once put on a belligerent attitude, rising on her hind legs and spreading her fangs. The male advanced very boldly and rising up likewise, he soon had her fangs caught on the spurs of his front legs. He did not raise her up much, but bent her upper half decidedly backwards so that her body was bent almost at a right angle. After a good deal of fumbling and tapping on the sternum of the female, the male introduced first the bulb of the left and later that of the right palpus. After withdrawing the latter, he waited for about one-half minute, and then very deliberately he withdrew from the female. Mating occupied about one minute's time. The female made no attempt to attack the male after the mating act.

When this male mated the second time, twenty-four hours after the making of the sperm web, he introduced both palpi twice. This has been observed in several instances.

When putting a male and a female together in an attempt to observe mating, it is well to make one of them move until it touches the other. This not only apprises them of each other's presence, but also reveals at once the inclination or disinclination for mating. If mating is to take place, they will proceed at once; if not, no amount of coaxing will induce them to do so. Frequently when the male has just touched the female with one of his front legs, and she does not show any visible response, he will slap her vigorously several times, which brings prompt action. She at once rises, spreads her fangs, and the male proceeds. When the male has just secured the fangs of the female in his spurs, she usually stands quite erect. At the introduction of the bulb of the first palpus she relaxes so that the abdomen may touch the ground.

In the majority of the matings that have been observed the female made no serious effort to attack the male at the close of the act. However, the male is almost always very careful in his departure. He moves away as far as possible before he releases her fangs and then he retreats very hastily.

The males of *Dugesiella hentzii* that Dr. Petrunkevitch observed all died toward the end of the month of November. The same has been observed in most of the males of *Eurypelma californica*. One of the males taken in the fall of 1923 lived till the 26th of the following July. This year (1927) one of the males brought in from the field lived till December 27. The male RT_1 is still living, and judging by his present condition, he will live through the winter. It may perhaps be

assumed that the unusual prolongation of the life of this male is due to the regular and abundant food supply furnished during the last four years of his life.

Soon after the mating season the males begin gradually to fail. The abdomen begins to shrink slowly, and the spider gets more and more sluggish. Finally the abdomen is nothing more than a shrivelled and deeply wrinkled prolongation of the cephalothorax, yet the male with the legs drawn up close to the body will live on for several days or even a week. It seems an excellent picture of death due to old age, a gradual and complete exhaustion of all the sources of energy.

The females present a very different picture. At the age of eleven they are probably not even mature. Records, as yet not quite complete, show that the females become sexually mature when twelve or thirteen years of age. One female that was brought into the laboratory when fully matured, fourteen to sixteen years old, is now, nine years later, still in a very healthy and vigorous condition.

SUMMARY

The tarantula, *Eurypelma californica*, common in a number of the southwestern states, has been under observation for about nine years, with the result that the life cycle and the mating habits of the male are fairly definitely known. The life cycle from hatching till sexual maturity is about eleven years, with the possible variation of one year more or one year less. During this time, a male undergoes about twenty-two molts. Until the last molt the male is indistinguishable from the female.

As many as four sperm webs are made by one male, indicating that he will mate at least four times. In the preparation for mating the stimulation of the sex glands is so thorough and deliberate that it seems strange for so low a form of animal life. Mating has been observed ten to twelve times.

After the mating season the males soon decline in vigor. Shrinking and becoming more and more sluggish for some time, they die apparently as a result of a total exhaustion of all sources of energy.

The females, judging by records not quite complete, become mature when twelve or thirteen years old. After attaining maturity, they will live for a number of years; it is not known how many, but certainly till they are twenty years old and probably much older.

LIST OF LITERATURE

Baerg, W. J. 1922. Regarding the habits of tarantulas and the effects of their poison. Scientific Monthly, vol. xiv, no. 5, pp. 482–489, 4 figs.

———. 1926. Regeneration of appendages in the tarantula, *Eurypelma californica*. Annals Ent. Soc. America, vol. xix, no. 4, pp. 512–513.

Bölsche, Wilhelm. 1927. Das Liebesleben in der Natur. Erster Teil, pp. 356–369.

Brazil, Vital. 1926. Contribucão ao estudo do veneno das Aranhas. *In* Memorias do Instituto do Butantan, Tomo III, Fasciculo Unico, pp. 34–41, pls. 18–20.

Ewing, H. E. 1918. The life and behavior of the house spider. Iowa Academy of Science Proc., vol. xxv, pp. 177–204, 11 figs.

Petrunkevitch, Alexander. 1911. Sense of sight, courtship and mating in *Dugesiella hentzi* (Girard) a Theraphosid spider from Texas. Zool. Jahrb. Abt. f. Syst. Geog. und Biol. d. Tiere, Bd. III, pp. 355–375, pls. 10–11, 4 figs.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

HUMAN SAPIENCE

Being a review of *The Abilities of Man: their Nature and Measurement*. By C. Spearman, Ph.D., F.R.S. New York (Macmillan), 1927. $5\frac{3}{4} \times 8\frac{5}{8}$; x + 415 + xxxiii. $4.50.

By Charles P. Winsor, Institute for Biological Research, The Johns Hopkins University

In this book Professor Spearman sets forth his theory of the nature of mental abilities and their variation. This theory was originally put forward by him in 1904, and has been the subject of much debate and controversy ever since. The present work is an exposition of the doctrine and of its present status, intended, one gathers, primarily for the general reader, although there is an appendix giving the principal mathematical demonstrations involved. There is no bibliography.

Professor Spearman begins with a survey of the different theories of mental ability heretofore popular. The most important of these is probably that which "assumes mental ability to lie under the sovereign rule of one great power named 'intelligence.'" Unquestionably, in ordinary life we classify people as clever, stupid, or otherwise, exactly as we call them tall or short. But where we can refine our judgments of height by measuring stature in inches or centimeters, such refinement in the matter of intelligence is less simple. However, mental tests were devised and applied and the results were considered as measuring intelligence. These tests, in one form or another, have been and are being used for all sorts of purposes, and some of their more enthusiastic advocates consider that their possibilities are almost unlimited. For instance, I quote the following from Goddard (Goddard, *Human Efficiency and Levels of Intelligence*. 1920, p. 127): "The intelligent group must do the planning and organizing for the mass, that our whole attitude toward lower grades of intelligence must be philanthropic. . . . Democracy is not impossible even in a group with a large mass of people of relatively low mentality, provided that there is a sufficiently large group of people of high intelligence to control the situation." Such quotations could be multiplied indefinitely; the feeling has been general that we might shortly expect a set of tests which would place everyone in his

proper pigeon hole, to the greater happiness and prosperity of the race.

Unfortunately, there are serious objections to the whole test procedure. As yet, we have no agreement on a definition of what intelligence is. Which mental activities involve it, and which do not? For example, shall we include memory? We find no general agreement. Some testers include it, others exclude it. We even find such authorities as Terman and Thorndike including it at one time and omitting it at others. Again, what about imagination? Or language? Or the power of attention? Or even motor ability? All these are included or omitted, depending on the individual tester. Even sensory perception has advocates on both sides. There is, in short, no agreement as to what constitutes intelligence, or in what mental operations it is to be looked for.

We even find the plea advanced by Terman that it is unreasonable to expect us to define intelligence; that we can measure it without knowing anything about its ultimate nature, just as a physicist can measure an electric current by means of a galvanometer without knowing what the ultimate nature of electricity is. But, as Spearman points out, the physicist knows where to look for his current; he knows that he must read the galvanometer which is in circuit with his current. If he did not know which of his galvanometers was really in the circuit, and had no means of finding out, he could determine very little about his current. In the same way, if we do not know which tests involve intelligence, we can hardly expect to measure it.

Naturally, attempts have been made to remedy this ambiguity. Definitions have been proposed, but without great success. Spencer's definition has often been used—intelligence is that mental power which produces "conscious adaptation to new situations." But we have here introduced two more terms—"adaptation" and "situation"—which, as Spearman shows, are themselves interpreted according to the fancy of the individual psychologist. But even without this, the definition does not tell us what kind of operation produces adaptation, and we are as much at sea as before. Other definitions, to which the same objections apply, are the following: "The power of good responses from the point of view of truth;" "the ability to act effectively under given conditions;" "that which can be judged by the degree of incompleteness of the alternatives in the trial and error life of the individual;" "a biological mechanism by which the effects of a complexity of stimuli are brought together and given a somewhat unified effect in behaviour." One feels that Professor Spearman is right when he advocates abandoning the term "intelligence" as having lost any definiteness it may once have possessed.

But in addition to all this, and supposing that we have defined our "intelligence" satisfactorily, still we have the task of establishing the unity of function of intelligence. But this is just what is probably not true, if we are to accept the results of the tests; for these tests are reported to measure many different functions, so that a high total score tells us nothing about which functions are working well. And worse, each investigator has his own set of functions into which "intelligence" may be analyzed.

The forced abandonment of the unitary "intelligence" leads naturally to the theory that there are broad mental powers, such as "judgment," "memory," "invention," "attention," each of which functions as a unit. Here, again, we have a doctrine which is widely held in the popular mind. In fact, in practice most of us

hold both the previous doctrine of "intelligence," and the contradictory doctrine of "faculties." We talk glibly of our friends' "judgment," "concentration," "imagination," or what not, just as we speak of their intelligence. As soon as we attempt to make the conception of faculties more definite, however, we find ourselves involved in difficulties. There is no general agreement as to what faculties should go on our list; no two psychologists would agree; and as soon as we have invented a list, some other worker can show that some of the faculties which we have considered as functional units ought really to be analyzed further.

The logical conclusion to which this process of analysis leads us is that there exist innumerable elementary abilities, which may be either independent or intercorrelated. Those who adopt this view attempt to justify their mental testing procedure on the ground that they thus secure an average sample of a person's abilities. Spearman points out here that for our average to have any meaning it must be based on a really representative selection, in which all abilities are represented, and in which duplication is avoided. This, however, is just what the present tests do not do. There is not really representative selection. There cannot be, for there is no agreement as to the elementary abilities which are to be tested. Further, there is the question as to whether such a sample would really have any great meaning if we obtained it.

That there is some meaning in the current mental testing is, however, obvious. The curious fact is that tests based on widely different theories, and apparently of widely different forms, do show substantial correlations with each other. Some theory is required to unify the facts. Having disposed, to his own satisfaction, of all the rival theories, Spearman advances his own.

Stated in its simplest terms, the theory is that the achievement of any individual x in any ability a is a linear function of two factors g and s, g being common to most if not all abilities, and s being specific to each ability. Put otherwise, the observed correlation between activities is usually due to the g, which is common to all of them, and only rarely to the fact that they share an s. Or, mathematically, we may write

$$\left.\begin{aligned} m_{ax} &= r_{ag}\, g_x + r_{as_a}\, s_{ax} \\ m_{bx} &= r_{bg}\, g_x + r_{bs_b}\, s_{bx} \\ &\cdots\cdots\cdots\cdots \end{aligned}\right\} \text{for any individual } x \quad (1)$$

$$\left.\begin{aligned} m_{ay} &= r_{ag}\, g_y + r_{as_a}\, s_{ay} \\ &\cdots\cdots\cdots\cdots \end{aligned}\right\} \text{for any individual } y$$

Such a system we shall refer to as a (g, s) system.

Now if we accept this theory, certain results can be derived from such a set of equations. We assume that the correlations of g with any s, and of one s with another, are all zero. Then the correlation of one ability with another will be due entirely to g, and we can show, with a little algebra, that

$$r_{ab} = \frac{r_{ag}\, r_{bg}\, \sigma_g^{\,2}}{\sigma_a\, \sigma_b},\ r_{ac} = \frac{r_{ag}\, r_{cg}\, \sigma_g^{\,2}}{\sigma_a\, \sigma_c}, \text{ etc.,}$$

and that

$$r_{ab}\, r_{cd} - r_{ac}\, r_{bd} = 0 \qquad (2)$$

The quantity on the left of equation (2) is termed by Spearman the "tetrad difference" of the correlations involved. We shall write (ab, cd) for this quantity. It is, of course, evident that four abilities will (by permutation of the subscripts) give us six tetrad differences, three of which will be numerically equal but of opposite sign to the other three.

The importance of the tetrad difference in Spearman's theory is that he makes it the criterion by which the whole theory is to be judged. It has been shown that if

$(ab, cd) = 0$ for all tetrads obtained from a table of correlations, then the abilities involved can be analyzed into a (g, s) system, and that if $(ab, cd) \neq 0$, no (g, s) system can be found; we shall require some more complicated system. Spearman's procedure in any given case, then, is to construct a table showing the intercorrelations of abilities, as measured by tests or otherwise, and to determine whether or not the tetrad difference vanishes. If it does, the abilities involved can be analyzed into the form of equations (1).

In practice, of course, the correlations which we obtain will always be affected by sampling errors, and accordingly our tetrad differences will not in general be zero even if they are derived from a (g, s) system, but will tend to fluctuate around zero. It therefore becomes important to determine the permissible range of fluctuation within which we may regard the tetrad difference as sensibly zero. This requires, clearly, determining the theoretical standard deviation of a tetrad difference in terms of the correlations on which it is based. This can be done by the usual procedure; and Spearman proceeds to make comparisons of the observed values of his tetrad differences with the theoretical probable error (derived by the usual convention that the p.e. $= 0.6745\ \sigma$). Now this assumes, among other things, that the frequency distribution of tetrad differences is approximately normal. This, however (as was pointed out in a review in *Nature*, August 6, 1927, pp. 181–183) is by no means even a plausible assumption. We know that, for small samples and for even moderately large correlations, the frequency distribution of correlation coefficients is widely different from the normal. Further, in a table of tetrad differences, the individual differences have correlation (over and above that due to their limited number) due to the fact that the same correlation coefficient enters into different tetrads. Thus the presence of a common element will introduce correlation between such quantities as (ab, cd) and (ae, fg). What kind of frequency distribution might result is by no means obvious; but to assume it Gaussian seems clearly unjustified until we have at least experimental evidence that it is approximately so. We should feel easier in our minds if Professor Spearman had given a frequency distribution of tetrad differences for a set of correlations actually known to be derived from a (g, s) system.

Professor Spearman does, however, give us something upon which to form an idea of how tetrad differences may vary. He has taken two tables of correlations of mental tests, in one of which 14 tests were applied to 37 persons, and has worked out the frequency distribution of tetrad differences for the two cases. Upon the frequency distributions so obtained he places normal curves having standard deviations equal to the theoretical and mean standard deviations of the tetrad differences of his tables. Graphically, the fit is good; but unfortunately he gives only a graphic comparison. The reviewer in *Nature*, cited above, stated that an actual goodness of fit test indicated that the fit is really very bad in one case, and distinctly not good in the other.

Hoping to obtain more light, I have myself calculated for the correlations of W. Brown, cited by Spearman (p. 147) the frequency distribution of tetrad differences. In this case I find that a normal curve will not give even an approximate fit; and that even the Pearson Type VII curve indicated by the values of the observed moments is an extremely bad fit to the data. On the other hand, the difficulty in the fit is that the tetrad differences are more closely concentrated about

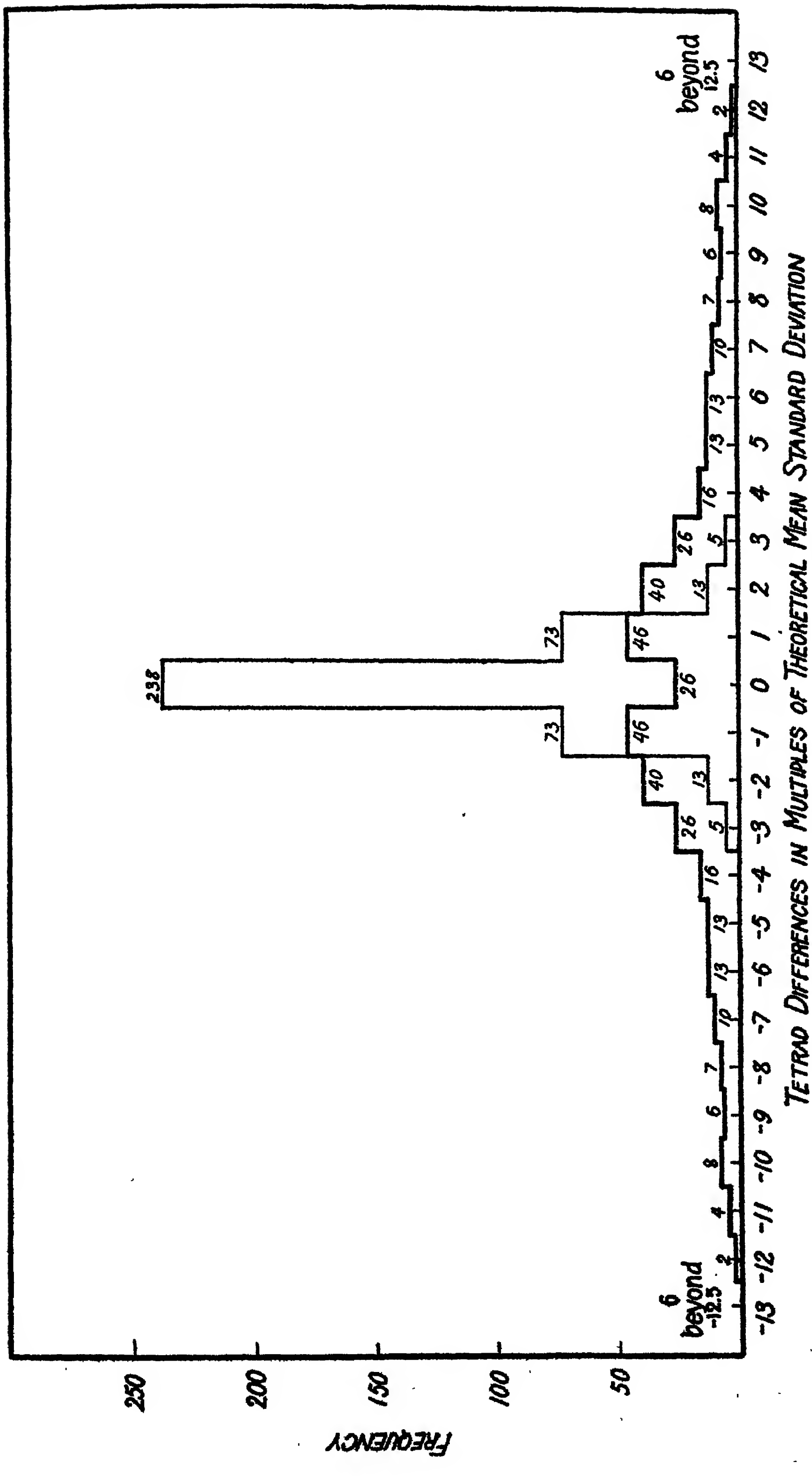


FIG. 1. COMPARISON OF FREQUENCY DISTRIBUTIONS OF TETRAD DIFFERENCES FOR MENTAL TESTS (BROWN) AND FOR PHYSICAL TRAITS OF MATURITY (GATES).

zero than the normal curve calls for; and accordingly we can hardly conclude from this that their true value is not zero.

Comparison of frequency distributions of tetrad differences for mental tests (Brown) and physical traits of maturity (Gates)

(Calculated from Spearman, pages 143 and 147)

CLASS INTERVALS	NUMBER OF TETRAD DIFFERENCES		NOTES
	Brown	Gates	
0 – 0.5	119	13	The class intervals are in
0.5– 1.5	73	46	terms of the theoretical mean
1.5– 2.5	13	40	standard deviation of a tetrad
2.5– 3.5	5	26	difference. This has the follow-
3.5– 4.5		16	ing values:
4.5– 5.5		13	Brown's correlations 0.0524
5.5– 6.5		13	Gates' correlations 0.0333
6.5– 7.5		10	The table gives only positive
7.5– 8.5		7	values of tetrad differences; the
8.5– 9.5		6	distribution is symmetrical, as
9.5–10.5		8	shown in the curve.
10.5–11.5		4	The class 0 to 0.5 covers only
11.5–12.5		2	a half interval in the table; the
over 12.5		6	corresponding class in the figure
			covers the full interval from
			−0.5 to +0.5

Spearman also presents an interesting comparison in the distributions of tetrad differences for a set of correlations of bodily dimensions (McDonnell, *Biometrika*, 1901, 1) and of physical traits taken as indicating degree of maturity (Gates, *Journal of Educational Research*, 1924, p. 341). These distributions are of an entirely different character from those of mental tests previously mentioned. Using as our standard of measurement the theoretical mean standard deviation of a tetrad difference (derived by the formula given by Spearman in his appendix) we find the scatter of the mental tests is very much less than that of the physical measurements. A comparison of the two indicates that the system of causes in one case must be radically different from that in the other. For purposes of comparison, I offer the distributions for the tetrad differences of Brown and for those of Gates. It will be noted that the unit of measurement in each case is the mean standard deviation of a tetrad difference, derived by Spearman's formula 16A, Appendix, p. xi. Clearly, the two distributions are not even remotely similar. The comparison, of course, proves nothing as to the causes in either case, except that they must be different in the two cases.

We now turn to a consideration of Professor Spearman's theory in more detail. Clearly we should properly consider his mathematics at some length. We shall, however, confine ourselves to a few general questions, which seem to us fundamental. For the rest, the mathematical proofs involved seem formally correct enough; but unfortunately, a mathematical proof is only as sound as its initial assumptions, and it is by no means easy for the present reviewer to determine precisely what Professor Spearman has assumed. One thing, however, appears reasonably clear; Professor Spearman assumes throughout that his fundamental relations are linear. We have, for example, the equation

$$m_{ax} = r_{ag}\, g_x + r_{as_a}\, s_{ax}$$

where we might expect

$$m_{ax} = f\,(g_x,\ s_{ax})$$

the determination of the form of the function being one of the problems to be solved. To this Professor Spearman would doubtless reply that in fact we have assumed nothing of the sort; we have shown that when (ab, cd) is zero, we can always write (1). This, as far as it goes, is true; but does not the proof involved assume that the correlations r_{ab}, etc., result from linear relationships? Have we not assumed

linear regressions throughout, and is the assumption justified? For example, has any adequate test been made to show that the regression of, say, "Cancellation" on "Opposites" is really linear? There is nothing in Spearman's book to tell us.

To return to our g and s, however, there are other remarks which seem pertinent. First, we should observe that the validity of the decomposition of variables into a (g, s) system does not depend in the least on whether there truly exist any physical or mental realities corresponding to g and s. They need be nothing more than a convenient mathematical fiction; and their values will be just as determinate. The best proof of such a statement is a demonstration that a system of variables can be devised which can be produced both by a (g, s) system and by a completely different system.

Suppose four variables, having the intercorrelations shown:

	A	B	C	D
A		0.895	0.694	0.578
B	0.895		0.633	0.517
C	0.694	0.633		0.408
D	0.578	0.517	0.408	

In this table the tetrad differences are all zero, and accordingly we should be able to split the variables into a (g, s) system; which we can do, according to Spearman's equations, with the following results:

$$
\begin{aligned}
m_{ax} &= 0.994g_x + 0.106s_{ax} \\
m_{bx} &= 0.899g_x + 0.438s_{bx} \\
m_{cx} &= 0.702g_x + 0.712s_{cx} \\
m_{dx} &= 0.578g_x + 0.814s_{dx}
\end{aligned}
$$

But we can equally well suppose these correlations to have arisen from the following system

$$
\begin{aligned}
m_{ax} &= v_{1x} + v_{2x} \\
m_{bx} &= v_{1x} + v_{3x} + v_{4x} \\
m_{cx} &= v_{1x} + v_{2x} + v_{3x} + v_{5x} \\
m_{dx} &= v_{1x} + v_{2x} + v_{3x} + v_{5x} + v_{6x}
\end{aligned}
$$

in which v_1, v_2, etc., are independent variables (having, in this case, equal standard deviations). And, as may be inferred, an infinite number of other decompositions are possible. It is to be observed also that any system of correlations can be represented by such a system of variables, whether or not the tetrad difference is zero.

This possibility is, of course, not overlooked by Spearman. He points out, first, that the (g, s) system differs from our (v) system in being unique; there is one and only one (g, s) system which will satisfy the conditions. Second, he points out that a relation can be set up between the (g, s) system and such a (v) system, whereby we can determine the (g, s) values from the (v) values. Finally, he urges that the (g, s) system is simpler and requires fewer assumptions, and accordingly should be given preference. With this question, however, we need not concern ourselves. We have merely pointed out that there is no necessary physical reality corresponding to the mathematical analysis. An analogy would be the decomposition of a velocity into component velocities which add by the parallelogram law, or the decomposition of an alternating current into components in quadrature with each other—one of the most useful devices in the theory of alternating current circuits. Unless and until we have evidence of the existence of g and s from some other source than the tetrad equation, we must regard them fundamentally as mathematical expressions and not as physically existing quantities.

Obviously, however, this should not prevent our using g and s if they are useful to us. The fact that the decomposition of velocities is an artifice of mathematics does not make it less useful. And, in Spearman's view, there are grounds for

believing in the physical existence of g and s.

Another point which seems important is the following. Professor Spearman writes $m_{ax} = r_{ag}\, g_x + r_{asa}\, s_{ax}$, in which r_{ag} and r_{asa} are constant for all individuals. Now, even if we allow that the relation connecting m_a with g and s is linear for any individual, it seems to involve an additional, and a rather considerable, assumption to say that the relation shall be the same for all individuals tested. Assuming that g and s really correspond to physical quantities, is there *a priori* any reason for assuming that they must have the same coefficients for all individuals tested? Must we have

$$m_{ax} = r_{ag}\, g_x + r_{asa}\, s_{ax}$$

and

$$m_{ay} = r_{ag}\, g_y + r_{asa}\, s_{ay}$$

rather than this relation?

$$m_{ax} = Ag_x + Bs_{ax}$$
$$m_{ay} = Cg_y + Ds_{ay}$$

Of course, we return immediately to the proof of the existence of the (g, s) system provided (ab, cd) vanishes throughout. However, it appears that Spearman himself recognizes that r_{ag} and r_{asa} remain constant only so long as the populations tested are sufficiently homogeneous. We find him saying (p. 217 *et seq.*): "Another important influence upon the saturation of an ability with g appears to be the class of person at issue. The most drastic example of this is supplied by a comparison between normal children and those who are mentally defective. . . . . The correlations are much smaller in the case of the normal children. This indicates that with these the influence of the energy [g] has gone down and that of the engines [s] has correspondingly gone up. . . . . No less marked is the tendency on comparing children with adults. As exemplifying this may be taken the correlations obtained by Otis and Carothers respectively for what appear to have been similar tests in each case:

TESTS	CORRELATIONS WITH g	
	Otis, Grades IV–VIII	Carothers' students
Analogies	0.84	0.71
Completion	0.88	0.53
Directions	0.86	0.45
Digits, memory	0.41	0.22

"Similarly, Stead has found that even motor abilities have considerable correlations with tests of g up to about 11–12 years of age, but not later."

We seem to find, then, that while in deriving our theory we showed that r_{ag} and r_{asa} should be constant for all individuals, in actual practice they vary from group to group. But if from group to group, why not within the group? In fact, we find Spearman going on from what we have just quoted as follows (p. 219): "Now, all the changes we have been considering follow a general rule. The correlations always become smaller—showing the influence of g on any ability to grow less—in just the classes of persons which, on the whole, possess this g more abundantly." But there seems to be no clear reason for supposing, if this is true for different classes, that it is not true for individuals within the class; and if this be true, it would appear that any theory which involved a linear relation between achievement, g, and s, could not be correct.

Of course, we still need not throw the theory overboard. It may well be that, provided we keep our group sufficiently homogeneous, we can maintain our linear relation; which amounts to saying that

for relatively small changes in *g*, the variation in achievement will be linear. But it would appear that for any complete theory we should require something much more elaborate than the linear (*g*, *s*) system.

So far we have not been concerned at all with what, if anything, *g* and *s* really are; with what physical facts they may be identified. Spearman, after rejecting the various explanations which have been made, suggests that we may regard *g* as a general mental energy, while the various *s*'s may be taken as the various engines in which this energy is utilized. The language, especially as applying to the engines, is somewhat vague; but Spearman nowhere, so far as I have found, explains his conception clearly. The hypothesis as stated seems scarcely likely to attract a physicist; to assume that output is given by the sum of the energy input and the efficiency of the engine is an unusual formula. We might, of course, say that we are dealing with logarithms; but there would appear to be difficulties here. In any case, the hypothesis seems scarcely of vital concern in the present state of the whole theory. If, of course, it were found possible to measure mental energy directly, the case would be different; but until we have some means for measuring it, it seems idle to waste much time identifying it with a factor *g*, whose very existence, even as a matter of mathematics, is still questionable.

There are other difficulties which will occur to any reader. One such lies in the highly variable nature of the measurements obtained, and of the results deduced from them. For example, on pages 202 and 203 Spearman cites the correlations with *g* which have been found by various workers for different tests. The test of "Opposites" appears three times, with correlations with *g* of 0.89, 0.71, and 0.37. Obviously, such values, if obtained in any biometric investigation, would indicate that something was radically wrong. Whether they really indicate that here, it is impossible to say, because we do not know that the three "Opposites" were really the same thing. However, we may reasonably infer from the fact that Spearman refers to them all under the same names, and without indicating in any way that they are different tests, that they are intended to be similar tests and to measure the same thing; and we are forced to conclude, either that the tests themselves were badly devised, or that the quantities correlated cannot be measured in this manner.

This difficulty, of the large variability of the measurements obtained in similar mental tests on the same subject, has of course attracted the attention of psychologists, and Spearman has devised a formula for eliminating its effect. This formula he calls the correction for "attenuation." The proof of it, and the circumstances under which it may legitimately be used, would lead us too far; and according to Spearman, it is unnecessary to use it in order to establish the vanishing of the tetrad difference. A remark of Spearman's about it (Appendix, p. i, note) may, however, be quoted: "It should be noted that the correction for attenuation only has, and only can have, the virtue of producing *on an average* the true amount of correlation. Hence, if this true amount is close on unity, the correction will in nearly half the cases produce values *greater than unity*, although no such amounts of correlation are actually possible." (Spearman's italics.) Without questioning the validity of the correction, one can merely report a certain uneasy visceral sensation when correlation coefficients greater than unity are mentioned.

We have devoted the bulk of this review to a consideration of the basic doctrine, and very little space is left for an exposition of the remainder of the book—which bulks rather larger than the portion we have examined. In the rest of the book Spearman builds his theory into an imposing edifice. This construction, however, rests entirely on the fundamental proposition that the decomposition of abilities into g and s is really valid. There are, however, some interesting results obtained. In particular, he devotes a good deal of attention to the search for general factors other than g common to numerous abilities. He claims to find such a factor (which he calls w) in the "consistency of action resulting from volition;" and he finds another factor, called c, whose precise nature is not quite clear, but which presents some interesting correlations with various traits of character. A selection of these (quoted from page 355) follows:

Sense of humor	0.98
Pure-mindedness	−0.45
Originality of ideas	0.88
Interest in religion	−0.39
Suggestibility	−0.29
Profoundness of apprehension	0.59

In conclusion, we may say that Professor Spearman seems to us to have fallen a long way short of establishing his theory. On the other hand, he has made out enough of a case to call for the serious consideration and investigation which his book will undoubtedly receive.

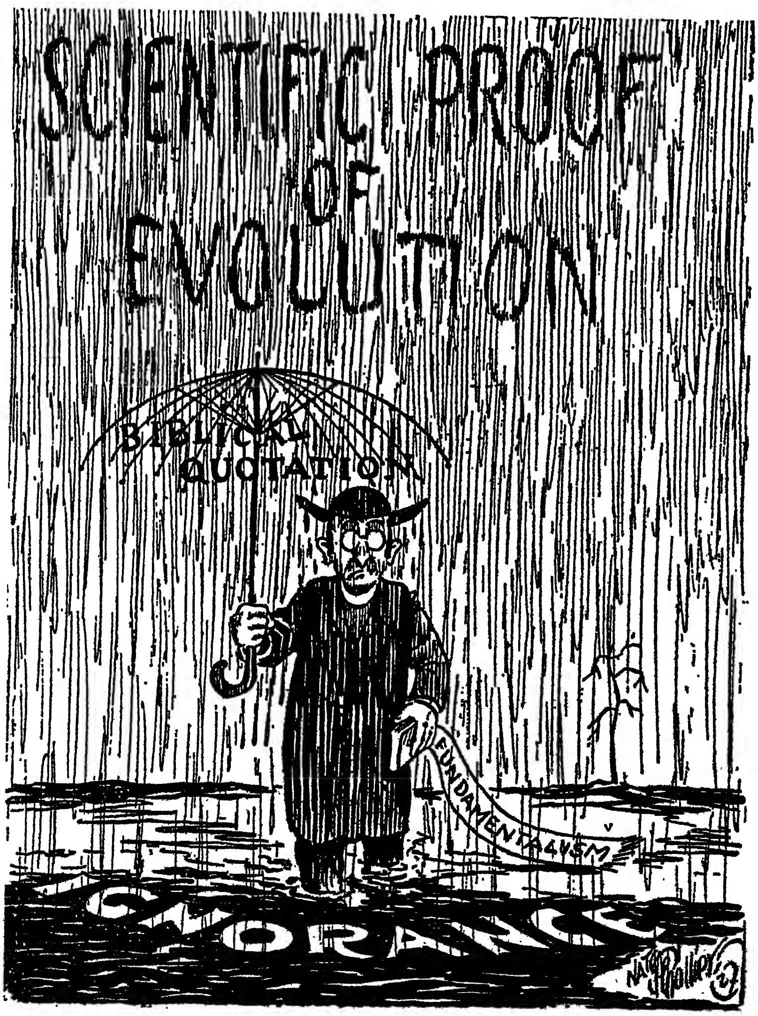
[The current issue of Biometrika (Dec. 1927, pp. 246–291) which appeared while this review was going through the press, contains a long analysis and criticism, by Pearson and Moul, of Professor Spearman's mathematics. The conclusion is there reached that the tests provided by Spearman are mathematically entirely inadequate to establish his theory; and in particular, that his formula for the standard deviation of a tetrad difference is in error. Accordingly, some of the statements made above may require qualification; but the conclusions reached still seem sound.]

BRIEF NOTICES

EVOLUTION

EVOLUTION.
Evolution Publishing Corporation
96 Fifth Ave., New York
Annual subscription $1.00
8 x 11

We are delighted to welcome this new journal, which has as one of its nobler purposes the exploitation of the fun in Fundamentalism. The cartoon which we reproduce here from the first issue is indicative of the earnestness with which this purpose is to be pursued. Reginald, our Office Boy, says he thinks it is too bad that they dressed the parson up in a Church of England uniform, instead of clothing suitable to the Baptist or Methodist he really is. We are disposed to agree with Reginald. The reverend clergy are by no means all Fundamentalists, and when one is embarking upon an organized



campaign of mayhem it is just as well to be discriminatory. If all the biblical brothers were as intelligent as, on the average, are those who perform the Episcopalian mysteries perhaps there would be no necessity for the evolutionary cohorts to gird their loins.

"Evolution" is going to be an entertaining little paper, if one may judge by the first number. David Starr Jordan, William K. Gregory, and Henshaw Ward contribute significant and readable articles and the editorial staff dresses up the number with merry and apposite jests. At a dollar a year a large subscription list ought to be readily obtained. Every teacher of biology can have great fun by giving his students access to this periodical.

THE SUPERFLUOUS MAN.
By Milton W. Brown.

Standard Publishing Co.
$2.00 $5\frac{1}{8} \times 7\frac{1}{2}$; 296 *Cincinnati*

It is stated in Who's Who that a lecture called "The Superfluous Man" has been delivered by Dr. Brown more than 1500 times. Now it is embodied in this book. It is difficult to characterize the book briefly because there are so many different kinds of things in it. We are not even quite sure who the superfluous man is, but A. E. Wiggam and E. G. Conklin seem to come in for the most extensive and severe disapproval. The chapter on "Intolerance" has entertained us most, because in it is developed the thesis that to forbid by law the teaching of organic evolution cannot justly be regarded as an act of intolerance. By a series of ingenious quotations from Conklin, Wiggam, and Coulter, coupled with the neat argument that when the evolutionist says that fiat creation is unthinkable he overlooks the fact that every artist does this very thing as a part of his job and that what such mere men can do will certainly be no difficulty at all for God, the reader is led to the following conclusion: "In view of the foregoing statement by a great scientist [Coulter], it becomes perfectly clear to the layman that the insistence, the great outcry about liberty of thinking, relative to the Tennessee law forbidding the definite teaching, as an established truth, that man descended from a lower order, is neither a limitation of intellectual freedom nor is it—as so many editorials have thundered—an outburst of fanatical ignorance."

There is a good deal of discussion of the problem of population, and again the novelty and unexpectedness of the conclusions reached must certainly amuse, even though they may fail entirely to convince the reader.

"The influence of the Christian church is to greatly increase the prosperity of its members, to impel them toward better living conditions, and hence the movement of population from the country and congested districts to the better residential districts, and the very sharp decline in the size of families.

"Christianity thus checks population through prosperity and happiness and enlargement. Thus Christianity ultimately cures the evil of overpopulation in a most happy way. While the earliest effect of Christian activities is indeed to save populations from starvation and pestilence, their full effect utterly corrects any threat to over-population."

The title of this book seems too subtle. We suggest that a more informative one would have been *Rotary-Kiwanian Fundamentalism, approved by George F. Babbitt and Elmer Gantry.*

THE WAR ON MODERN SCIENCE. *A Short History of the Fundamentalist Attacks on Evolution and Modernism.*
By Maynard Shipley. Alfred A. Knopf, Inc.
$3.00 5½ x 8¼; xiv + 415 *New York*

Mr. Shipley is president of the Science League of America, a body organized to fight Fundamentalism. This book is intended as a history of the progress of the campaign during the past five years, and, one must suppose, as insidious propaganda against the palaeobaptists. How much good it will do in the latter direction seems dubious. Obviously no Fundamentalist is going to alter his views as a result of reading it. Those who are not Fundamentalists need no converting. The real usefulness of the book in the long run will be as a well put together contemporary record of an ephemeral social disturbance in American life, more idiotic perhaps than most, but on that very account the more certain to be short lived. We wish Mr. Shipley all success in the good fight he is making to hasten the final interment.

THE ORIGIN OF SPECIES BY MEANS OF NATURAL SELECTION *or the Preservation of Favored Races in the Struggle for Life.*
By Charles Darwin. The Macmillan Co.
80 cents (cloth) *New York*
4¾ x 7⅛; xxxv + 557

A cheap, but good reprint of the sixth edition of the great classic of biology, with an interesting introduction by Professor Edmund B. Wilson.

GENETICS

SEGREGATION AND AUTOGAMY IN BACTERIA. *A Contribution to Cellular Biology.*
By F. H. Stewart. Adlard and Son, Ltd.
7s. 6d. 5½ x 8½; v + 104 + 4 plates *London*
(paper)

This book is the record of an interesting piece of research, which leads the author to a new theory of the life-cycle and of the origin of variation in bacteria.

If a bacterium

"is placed in new surroundings with sufficient food it multiplies quickly by simple fission (colony formation). This vegetative phase is stopped by an intrinsic force, but it can be either lengthened or shortened by external conditions (amount of food available, moisture, crowding) and it can be continued indefinitely by frequent change of surroundings.

"Shortly before vegetative growth stops the second phase of the life-cycle begins, in which a few out of the great number of bacteria in a colony (either on solid or in liquid nidus) go through segregation, autogamic conjugation, and, under certain circumstances, variation. In spore-bearing races the zygote forms the spore. Segregation in bacteria is the same as in the higher forms; in it allelomorphic couples of the organism divide. We know little about the mechanism of autogamy, but it seems not unlikely that before segregation takes place each allelomorphic couple is represented in the 'anterior' and 'posterior' halves of the bacterium (Schaudinn and Dobell's pre-sporing division), and that, after segregation, and if nothing disturbs them, the 'right hand' allelomorphs of one half of the body unite with the 'left hand' allelomorphs of the other. At least this is as good a mental picture as any other. But, if a definite external stimulus is at the moment bearing on a heterozygous bacterium, then in the one pair (anterior and posterior) of allelomorphic couples which is concerned with the stimulus, the dominant allelomorphs are dissipated (as primitive polar bodies?), the recessives come together, and the bacterium varies.

"The recessive so formed may also vary in simple fission if one of its recessive allelomorphs is not pure but is loaded with a fragment of the dominant factor. It may then vary in two directions—by increasing, or decreasing, this fragment."

TILLOTSONS DIRECTORY OF PEDIGREE STOCK BREEDERS AND YEAR BOOK OF THE BREEDING INDUSTRY. *An Index of Pedigree Stock Breeders and Owners in England, Wales, Scotland, Ireland, and the Channel Islands; Australia, New Zealand, British South Africa and Canada; and Year Book Concerning Breeds and Events in the Breeding Industry in Various Countries.*
Compiled and Edited by R. de Toll.
Tillotsons Publishing Co.
£1. 15s. $7\frac{1}{4}$ x $8\frac{3}{4}$; 812 *London*

The general scope of this useful work is sufficiently indicated by its title. Some of the numerous special articles in the volume are of real interest and value to the student of genetics, as are also the excellent photographic illustrations of breed types. It is a pity that the live-stock industry of this country has no annual of similar scope.

GENETICS IN RELATION TO AGRICULTURE.
By Ernest B. Babcock and Roy E. Clausen.
McGraw-Hill Book Co., Inc.
\$5.00 $5\frac{3}{4}$ x 9; xiv + 673 *New York*

This is the second edition, revised nearly to the point of complete rewriting, of what has come to be regarded as, on the whole, the best existing text book of genetics for teaching purposes. Its high reputation will be enhanced by its present form.

LE PROBLÈME DES TRANSFORMATIONS DES ÊTRES VIVANTS RÉSOLU EXPÉRIMENTALEMENT. *La mutation provoquée. Le mécanisme des mutations spontanées. La variabilité héréditaire des individus et la fixité des espèces. Nouvelles données de philosophie scientifique.*
By L. Rémy. *Gaston Doin et Cie*
10 francs $4\frac{1}{2}$ x 7; vii + 162 (paper) *Paris*

Mademoiselle Rémy furnishes in this book a brief, popular *résumé* of some of the elementary facts of modern genetics, Mendelian, mutation, etc. The results of some crossing experiments with peas are presented.

GENERAL BIOLOGY

INSTINCT IN THE CELL AND ORGANISM. *A Genetic Account of the Primal Urges, Impulses and Reactivities of Living Organisms. With Special Reference to the Evolutionary Development of the Human Psychic Life. In three Parts: I. The Instinctive Functionings of the Cell. II. The Genetic Development of the Psychic Powers. III. Instinct in the Development of the Social Life.*
By Neander P. Cook. *The Weimer Press*
\$5.00 6 x $9\frac{1}{2}$; xii + 244 *Alhambra, Calif.*

We are told in a four page abstract (sold for 10 cents) which accompanies this book that: "Probably no book of recent years contains such far-reaching new conceptions of fundamental importance in Biology." This naturally suggests turning the book over to Reginald the Office Boy for his tender ministrations. But before doing so we took the trouble to read it. As a result we are not quite so sure that the bold asseveration quoted has not got some element of truth in it. The author seems clearly to fall under Augustus DeMorgan's definition of a paradoxer. But if one neglects certain developments of the

theory as unnecessary and unsupported by any established biological facts, the residue is an interesting speculation with much to commend it to the attention of biologists. The central idea is that: "Instinctive reactivity, instinctive responses, instinctive urges, these are the moving impulses in living beings, whether we study them as unicellulars, as plants or animals, as lone hunters or in armies, as swarms, flocks, herds, hives, peoples or nations." Space is lacking here to show how this idea is developed. It must suffice to say that while perhaps no qualified biologist will agree with Mr. Cook at all points it will do none of them any harm to read what he has to say.

POULTRY PRODUCTION.
By William A. Lippincott. *Lea and Febiger*
$3.50 5¼ x 7¾; viii + 602 *Philadelphia*

The fourth edition, thoroughly revised, of a standard poultry text. It is one of the most scholarly books in the field, extensively illustrated, and well documented with a bibliography covering 20 pages of closely set 8-point type. The general biologist will find it a useful *résumé* of the considerable contributions which have been made by poultry workers during the last 25 years to the knowledge of avian physiology and genetics.

REGENERATION UND TRANSPLANTATION. *1. Band: Regeneration.*
By E. Korschelt. *Gebrüder Borntraeger*
M.60 6¾ x 10; xii + 818 (paper) *Berlin*

This is a colossal survey of the field of regeneration, thorough and systematic, as would be expected from its distinguished author. It is to be followed by a volume on transplantation and explantation, which is now in preparation. The painstaking thoroughness of the work is indicated by the fact that this first volume contains a bibliography covering 65 closely printed pages. The whole treatise will constitute a reference work which no biological laboratory can afford to be without.

FOUNDATIONS OF BIOLOGY.
By Lorande Loss Woodruff.
The Macmillan Co.
$2.50 5 x 7¾; xxiii + 546 *New York*

MANUAL OF BIOLOGICAL FORMS.
By George A. Baitsell. *The Macmillan Co.*
$3.50 5 x 7¾; xiv + 411 *New York*

The first of these volumes is the third edition, revised, of a widely used textbook of elementary general biology. The chief addition to this new edition is a chapter on biology in relation to human welfare.

Dr. Baitsell has also revised his text, which is intended to serve as a complementary work to Professor Woodruff's. It gives detailed descriptions and directions for study of the forms used in laboratory work in general biology.

The two books together furnish the basis of an excellent course.

GENERAL BIOLOGY. *A Book of Outlines and Practical Studies for the General Student.*
By James G. Needham.
American Viewpoint Society, Inc.
$2.50 5½ x 7½; xiv + 546 *New York*

The thirteenth edition of a standard and valuable text book. Professor Needham writes with a clarity, charm, and insight, rarely achieved by scientific men. These qualities are exhibited in high degree in this book as well as in his well-known text book of limnology *The Life of Inland Waters.*

THE MICROSCOPY OF DRINKING WATER.

By George Chandler Whipple. Revised by Gordon M. Fair and Melville C. Whipple.

John Wiley and Sons, Inc.

$7.00 *New York*

$5\frac{3}{4} \times 9$; xix + 586 + 19 plates

A fourth edition, revised after the distinguished author's death by two of his colleagues, of a book which has been a standard reference work for sanitary engineers and limnologists for nearly thirty years. A large amount of new material has been added throughout the book, and it has been brought up to date. It thus starts another long career of usefulness.

PHEASANT JUNGLES.

By William Beebe. *G. P. Putnam's Sons*

$3.00 $6 \times 8\frac{3}{4}$; xiii + 248 *New York*

For the material of this popular travel book the author draws on his experiences of a number of years ago in the jungles of Ceylon, Borneo, the Malay Peninsula, and the Himalayas, when he was collecting material for his monograph on the pheasants. The tale has all the charm of style and thrilling interest of matter which the public has come to associate with Mr. Beebe's writings on natural history.

MICROSCOPIC FRESH WATER LIFE.

By F. J. W. Plaskitt.

Chapman and Hall, Ltd.

13s. 6d. $5\frac{1}{4} \times 8\frac{1}{4}$; xi + 278 *London*

An elementary manual primarily intended for, and likely to be chiefly useful to, the amateur microscopist. It is abundantly illustrated, partly by photographs and partly by line drawings. The former are, on the whole, better executed than the latter.

HOW BIRDS LIVE. *A Brief Account of Bird Life in the Light of Modern Observation.*

By E. M. Nicholson.

Williams and Norgate, Ltd.

3s. 6d. $4\frac{3}{4} \times 7\frac{1}{4}$; x + 139 *London*

A very interesting popular account of the natural history of common birds, with a number of valuable original observations on bird populations, natural elimination, and other ecological topics. We highly recommend this little book to the attention of general biologists and students of evolution.

KINETIC THEORY OF GASES.

By Leonard B. Loeb.

McGraw-Hill Book Co., Inc.

$5.50 $5\frac{3}{4} \times 9$; xvi + 555 *New York*

A thorough, critical review of the present state of knowledge and opinion regarding the kinetic theory of gases. It is primarily intended for students of physics and chemistry, but will be a useful reference work for general biologists and physiologists. It is abundantly documented bibliographically, and has good indices.

DAS LEBEN IN FINALER AUFFASSUNG. *Abhandlungen zur theoretischen Biologie, Heft 26.*

By Eugenio Rignano. Authorized German edition by Paul Graf Thun-Hohenstein.

Gebrüder Borntraeger

2.70 marks $6\frac{1}{2} \times 10$; 35 (paper) *Berlin*

A German translation of a condensed statement of the author's well known vitalistic theory of the observed teleology in nature, with an introduction by Hans Driesch, saying, in effect, that while Rignano's brand of vitalism is not his brand, still all vitalism is good, and urging the reader to compare the two kinds.

THE LAWS OF LIVING THINGS.
By Edward J. Menge.
The Bruce Publishing Co.
$1.72 $5\frac{1}{4} \times 7\frac{3}{4}$; 530 *Milwaukee*

A high-school textbook of biology, which starts off with the perch as the standard type form, on which the discussion of other living things is hung. The book is extremely comprehensive though elementary.

HUMAN BIOLOGY

THE MOTHERS. *A Study of the Origins of Sentiments and Institutions.*
By Robert Briffault. *The Macmillan Co.*
$27.00 *New York*
$6 \times 9\frac{7}{8}$; Vol. I, xix + 781
II, xx + 789
III, xv + 841

This is a monumental and brilliant contribution to prehistory. The method is to re-examine the data available regarding the ethnography of primitive races of mankind, and from it synthetically to reconstruct the probable course of human social evolution from its earliest stages. The material which Mr. Briffault uses is old, and available to everyone. But what a thorough and critical combing-over he has given it! His contribution, apart from the colossal industry which the work has involved, is a fresh point of view. It is that: "The social characters of the human mind are, one and all, traceable to the operation of instincts that are related to the functions of the female and not to those of the male. That the mind of women should have exercised so fundamental an influence upon human development in the conditions of historical patriarchal societies is inconceivable. I was thus led to reconsider the early development of human society, of its fundamental institutions and traditions, in the light of the matriarchal theory of social evolution."

The author is thoroughly convinced of the overwhelming importance of sex in social life. And in prehistoric stages of culture he makes a very strong case that the interests and viewpoints of women played a much more important rôle than in any society now existing. The final conclusion reached is that: "The traditional inheritance of the human mind, if these considerations are well founded, has been moulded in the first instance not by the fierce passions of wild hunters battling for the possession of food and of women, but by the instincts of the mothers."

Every serious student of human biology should have this work on his shelves. Besides the intrinsic value of its contribution it is a reference work of first importance.

ARABIAN SOCIETY AT THE TIME OF MUHAMMAD. *Parts I and II.*
By Pringle Kennedy. *Thacker, Spink and Co.*
Rs. 7/8 $5\frac{1}{2} \times 8\frac{1}{2}$; vi + 253 *Calcutta*

This is an extremely interesting contribution to human biology. The point of view from which the analysis of the early history of Muhammadanism is undertaken is indicated by the following quotation:

> "Whatever the opinion one may have of this extraordinary man, whether it be that of the devout Muhammadan, who considers him the last and greatest herald of God's word, or of the fanatical Christian of former days, who considers him an emissary of the Evil one, or of certain modern Orientalists, who look on him rather as a politician than a saint, as an organizer of Asia in general, and Arabia in particular, against Europe, rather than as a religious reformer; there can be no difference as to the immensity of the effect which his life has had on the history of the world. To those of us, to whom the man is everything, the milieu but little, he is the

supreme instance of what can be done by one man. Even others, who hold that the conditions of time and place, the surroundings of every sort, the capacity of receptivity of the human mind, have, more than any individual effort, brought about the great steps in the world's history, cannot well deny, that even if this step were to come, without Muhammad, it would have been indefinitely delayed."

The book contains much matter of great interest to the sociologist, the psychologist, and the eugenist, as well as to the historian *sensu stricto*. It is interesting to learn, for example, that none of the sons of the first three Caliphs, Abu Bakr, Omar, and Othman, all of whom were indeed superior persons, "inherited their father's character."

THE HUMAN BODY.
By Logan Clendening. Alfred A. Knopf, Inc.
$5.00 6 x 9¼; xxii + 399 *New York*

THE HUMAN BODY.
By Trevor Heaton. E. P. Dutton and Co.
$3.00 5½ x 8; ix + 250 *New York*

These two books with the same title appear almost simultaneously, the first by an American practising physician, the second by an Oxford don. Both are sound, authoritative, well-written treatises intended to give the layman a clear and sufficient understanding of how his body is put together and how it works in health and in disease. Both serve this purpose incomparably better than any prior books in the field. They make both the old-fashioned "family doctor book" and the high-school "physiology and hygiene" look the sad, dull things that they were.

So far the two books travel along together. Then their paths begin to diverge. Dr. Clendening's book is vastly more entertaining, better and more extensively illustrated, and written with a Gargantuan dash, vigor, wit, and humor which leaves it with no real competitor whatever. He explodes ruthlessly all the popular superstitions about the body and its care which have held sway over the lay mind, and only in lesser degree over a good fraction of the collective medical mind, for many long ages. Altogether, Dr. Clendening has made a notable contribution to the joy of the world as well as to the store of common knowledge. His book will irritate the pedants and the uplifters, in and out of the medical profession, but we see no harm in that.

POPULATION PROBLEMS OF THE AGE OF MALTHUS.
By G. Talbot Griffith. The Macmillan Co.
$5.00 5½ x 8¾; 276 *New York*

In this extremely interesting and useful volume the author has attempted to reconstruct for modern eyes the statistical picture which Malthus had before him when he wrote his essay.

"This theory that an increasing population was in all cases desirable and necessary became an axiom which continued for some centuries, and discussions were always taking place as to the various means of securing this. Towards the end of the eighteenth century, when, in point of fact, the population was increasing with a rapidity hitherto unapproached, there was, owing largely to the failure to take a Census, a great feeling that the population was decreasing.

"It was into such an atmosphere that Malthus's *Essay on Population* burst. The continued absence of any reliable and official figures of the population heightened the surprise effect of the essay, and when in 1801 a Census was taken, it confirmed what Malthus had said about the increase of the population up to that time. The *Essay*, backed up by the Census, killed the axiom that under all circumstances an increasing population is desirable."

The book is a valuable contribution to the history of human biology.

DIE MESTIZEN AUF KISAR.
By Ernst Rodenwaldt. *G. Kolff and Co.*
I, xvii + 483 *Weltevreden*
II, tables and plates

This is a contribution of the very first importance to the research literature of human biology. It is a thorough, detailed, and comprehensive study of the anthropology, biology, and sociology of the European-native bastard people of Kisar, a small island in the so-called "Southwest Islands" group in the Dutch East Indies. The nearest large island is Timor. About the middle of the 17th century the Dutch took up residence on the island. The descendants of the original crosses between these Europeans and the natives inhabit the island today. They have been studied, family by family, in the most exhaustive manner by Dr. Rodenwaldt. One volume of the work is devoted to plates and pedigree charts. We congratulate the author on so fine a piece of work, and commend it to all students of human biology.

THE MYSTIC ROSE. *A Study of Primitive Marriage and of Primitive Thought in its Bearing on Marriage.*
By Ernest Crawley. Revised by Theodore Besterman. *Boni and Liveright*
$10 Vol. I, 5½ x 8½; xx + 375 *New York*
Vol. II, viii + 340

The original edition of this classic of ethnology has long been out of print. The material for this welcome reissue was to some extent revised by Mr. Besterman after the author's death, but mainly augmented by additions, consisting chiefly "first, of evidence, or further evidence, where the argument seemed to require strengthening, and of specimens of the large accumulations of anthropological material during the last two decades, and, secondly, of replies to criticisms and of discussions of the more recently advanced theories." There has also been added a bibliography covering 42 pages, and the index has been made more comprehensive and detailed. It is a real service to human biology to have made this treatise once more readily available.

CHILD LIFE INVESTIGATIONS. *Social Conditions and Acute Rheumatism. Medical Research Council Special Report Series, No. 114.*
By G. F. Still (and a Committee).
His Majesty's Stationery Office
2s. 6d. 6 x 9¾; 108 (paper) *London*

The general conclusion reached from this painstaking study of the environmental influences in relation to the incidence of acute rheumatism in children is: "That although it is difficult to point to this or that fault of environment as responsible for rheumatism, nevertheless it is by raising the standard of environment, improving the home conditions so that they approximate to the well-ordered conditions found in such institutions as those in which rheumatism was found to be much less common, and probably by reducing crowding, so that the possibility of contagion may be diminished, that we may hope to reduce the frequency of rheumatism in children."

THE ETHICS AND ECONOMICS OF FAMILY ENDOWMENT. *The Social Service Lecture, 1927.*
By Eleanor R. Rathbone. *The Epworth Press*
2s. 6d. net 5½ x 8; 118 *London*

The central thesis of this tract, delivered as an endowed lecture to the Wesleyan Conference, is that society as a whole should encourage the indigent, impoverished, and generally submerged portion of the population to have as many children

as they like, by the simple and efficient expedient of removing, at the public expense, any economic burden incident to rearing large families. This proposal is seriously made, and in the name of Christianity, by a women who is herself a citizen of a country in which the population increases by about 600 a day and in which something of the order of a million people are at all times unable to find work to keep themselves alive. We like the nerve of the proposal, but not much else about it.

THE END OF A WORLD.
By Claude Anet. Translated from the French by Jeffery E. Jeffery. Alfred A. Knopf, Inc.
$3.00 5 x $7\frac{1}{2}$; 268 *New York*

An entertaining romance, which attempts to portray through the medium of fiction the end of the prehistoric civilization which had its metropolis in what is now Les Eyzies. It is charmingly written. Some of the reconstructions of this lost civilization which the author imagines are plausible and seem probably true. Others are more dubious. It is almost certain that as more evidence accumulates some of the theories about the Solutrean and Aurignacian civilizations now prevailing in the best archeological circles will be modified. The book is illustrated with bold and rather effective black and white drawings from cave paintings and sculptures.

MAORI SYMBOLISM. *Being an Account of the Origin, Migration, and Culture of the New Zealand Maori as Recorded in Certain Sacred Legends.*
By Ettie A. Rout. Harcourt, Brace and Co.
$6.00 6 x $9\frac{1}{2}$; xxxii + 322 *New York*

Ettie Rout can be depended on to write vividly of whatever subject she tackles. This book has obviously been produced *con amore*. The dedication is to "my fellow-countrymen—the New Zealand Maori." It is a detailed, rather rambling, but extremely interesting discussion of Maori ethnology and folklore, based upon evidence given by "an Arawa Noble," Hohepa Te Rake. The material is discussed under five main heads: Origin and migration of the New Zealand Maori; health and race culture; social organization; agriculture and building; sacred life symbols. The book is extensively and well illustrated, and has a detailed index.

MENSCHLICHE ERBLICHKEITSLEHRE UND RASSENHYGIENE. *Band I. Menschliche Erblichkeitslehre.*
By Erwin Baur, Eugen Fischer, and Fritz Lenz. J. F. Lehmanns Verlag
16 Mk. 6 x 9; xii + 601 *München*

The third, revised and enlarged, edition of the best existing general book on human inheritance. The authors express the belief that not only has general genetic theory become stabilized but also human genetics, so that future editions of this book are not likely to require fundamental revision. It is a pity that we have in English no such sound, comprehensive, and stimulating work as this on human heredity.

THE PRINCIPLES AND PRACTICE OF MEDICINE. *Designed for the Use of Practitioners and Students of Medicine.*
By Sir William Osler. Tenth Edition, Thoroughly Revised by Thomas McCrae.
D. Appleton and Co.
$7.50 6 x 9; xxviii + 1233 *New York*

The "one volume Osler" is a classic of medical literature. It is full of the wisdom of "the Chief." Dr. McCrae is a

careful and conservative editor. In his preface to this tenth edition he quotes Osler's saying that "A Textbook is not a Year-Book," and says that he has endeavored to "retain the features characteristic of Sir William Osler." It is a great book and will long continue its useful service. For the human biologist who wants to find, in brief space, what is known about a particular disease and its treatment there is no better source than this.

IMMIGRANTS AND THEIR CHILDREN 1920. *A Study Based on Census Statistics Relative to the Foreign Born and the Native Whites of Foreign or Mixed Parentage. Census Monographs VII.*
By Niles Carpenter.
Government Printing Office
$1.50 $6\frac{3}{4}$ x 10; xvi + 431 *Washington*

An analysis of the population and birth data of 1920 relative to racial origins. The study follows lines somewhat similar to those of Pearl in his "Vitality of the Peoples of America," and confirms his principal conclusions. But this investigation is more comprehensive in its scope. It is done with critical care and deserves the attention of all students of human biology.

THE ANGLO-SAXONS IN ENGLAND *During the Early Centuries After the Invasion.*
By Nils Aberg. *W. Heffer and Sons, Ltd.*
12s. 6d. *Cambridge*
$6\frac{1}{2}$ x 10; vii + 219 (paper)

An interesting, finely printed and illustrated treatise on Anglo-Saxon archeology, based largely upon English museum collections of metal artefacts.

TRENDS OF POPULATION IN THE REGION OF CHICAGO.
By Helen R. Jeter.
The University of Chicago Press
$2.50 $8\frac{1}{2}$ x 11; xv + 64 *Chicago*

This is a detailed statistical study, with numerous graphs, of the growth of the population of Chicago and surrounding urban and rural areas. The study was made for the Chicago Regional Planning Association. Predictions of future population up to 1950 are included.

ALLGEMEINE KONSTITUTIONSLEHRE *in Naturwissenschaftlicher und Medizinischer Betrachtung.*
By O. Naegeli. *Julius Springer*
Rm. 9.60 *Berlin*
$6\frac{1}{4}$ x $9\frac{1}{2}$; iii + 118 (paper)

A brief but comprehensive review of human genetics and the constitutional factors in disease. The book will be found useful by the medical student or practitioner who cannot give the time necessary for the perusal of Bauer's standard work on the subject.

EVOLUTION OF PREVENTIVE MEDICINE.
By Sir Arthur Newsholme.
Williams & Wilkins Co.
$3.00 5 x $7\frac{1}{4}$; xv + 226 *Baltimore*

A brief outline, illustrated with portraits, of the history of public health and preventive medicine. The book would have been more useful to the serious student if there had been included a bibliography giving precise citations to the sources used.

ZOOLOGY

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferungen VI, VII, VIII, IX.* *Edited by G. Grimpe and E. Wagler.*

Akademische Verlagsgesellschaft M. B. H. *Leipzig*

Lieferung VI, M. 16.80
6 x 8½; 212 (paper)
Lieferung VII, M. 10.80
6 x 8½; 136 (paper)
Lieferung VIII, M. 14.60
6 x 8½; 186 (paper)
Lieferung IX, M. 13.60
6 x 8½; 146 (paper)

These four parts maintain well the standard set in earlier numbers of this collective work on the fauna of the North and Baltic Seas, which have already been noticed in The Quarterly Review of Biology as they appeared. The groups discussed in these numbers are as follows: *Epicaridea*, by F. Nierstrasz and G. A. Brender à Brandis; *Stomatopoda* and *Decapoda*, by H. Balss; *Gadiformes* and *Cyclostomi*, by W. Schnakenbeck; *Ctenophora*, by T. Krumbach; *Leptostraca*, by J. Thiele; *Elasmobranchii* and *Chondrostei*, by E. Ehrenbaum; *Tintinnidae*, by E. Jörgensen; non-parasitic *Copepoda*, by O. Pesta; *Cirripedia*, by P. Krüger; *Branchiostoma*, by V. Franz; *Oligochaeta*, by W. Michaelsen; *Thaliacea*, by J. E. W. Ihle; *Teleostei Physostomi*, by H. M. Kyle and E. Ehrenbaum.

L'INFECTION MICROBIENNE ET L'IMMUNITÉ CHEZ LA MITE DES ABEILLES, *Galleria mellonella*.

By S. Métalnikov. *Masson et Cie*
18 francs 6½ x 10; 139 (paper) *Paris*

This is an extremely interesting monograph on the wax moth (*Galleria*), which seems likely to become a useful laboratory animal. Perhaps the most interesting biological peculiarity of this odd animal is its ability to digest beeswax, and utilize it as its chief source of nourishment. The principal object of the monograph is the study of immunity in *Galleria*. Acquired immunity is easily obtained, and is stated to be transmissible to succeeding generations. As might be expected *Galleria* is able to digest easily the waxy envelope of the tubercle bacillus. This fact opens up some interesting possibilities of research. Biologists will want to read this monograph, even though they are not primarily interested in the special problems of immunity.

REPORT ON CETACEA STRANDED ON THE BRITISH COASTS FROM 1913 TO 1926.

By Sir S. F. Harmer.

British Museum (Natural History)
7s. 6d. *London*
9¼ x 12; 91 + 7 maps (paper)

This is the author's tenth, and last, report in an interesting series, which has contributed much to knowledge of the Cetacea. While primarily having to do with stranded whales this present report amounts to a general discussion of the biology of Cetacea. For the specialist the principal result is "the record of the seasonal and local occurrences of the several species, each of which has definite partialities as to time and place. Stranded specimens cannot indeed be expected to give full information on these subjects, but it is found that each year examined gives on the whole the same results as its predecessors, and the evidence thus obtained need not be ignored."

The report is rather fully illustrated, and contains a key for the determination of British whales and dolphins and a short bibliography.

HOST-PARASITE RELATIONS BETWEEN MAN AND HIS INTESTINAL PROTOZOA.
By Robert Hegner. *The Century Company*
$3.50 $5\frac{3}{4} \times 8\frac{3}{4}$; xiii + 231 *New York*

This is the first volume in the Century Biological Series, of which Dr. Hegner is general editor. The purpose of the book is "to gather together the more relevant data regarding the host-parasite relations of the intestinal protozoa of man and to present them in logical order in such a way as to bring out the state of our knowledge with special reference to the desirability of further studies." The treatment is excellent, but there is a sparseness of illustrations for which there seems no compelling reason. There is a bibliography of 25 pages, and author and subject indices. We extend a hearty welcome to the series which this volume inaugurates at a high level of excellence.

ECONOMIC BIOLOGY FOR STUDENTS OF SOCIAL SCIENCE. *Part I. Harmful and Useful Animals.*
By Philippa C. Esdaile.
University of London Press
7s. 6d. $5\frac{1}{2} \times 8\frac{1}{2}$; xv + 175 *London*

Specialization goes ever further and finer. Here we have an elementary zoölogy for students of what we call in this country "domestic science." It picks out for description and illustration (both excellent) those animals and plants "which are, or may be, closely associated with man and his household." The present Part I deals with animals, such as bath sponges, pin-worms, bed bugs, cockroaches, spiders, etc. Part II will discuss "Animal and Vegetable Products." The book should serve extremely well the class for which it is intended. And furthermore every householder will find it an interesting book to have about.

SEASHORE ANIMALS OF THE PACIFIC COAST.
By Myrtle R. Johnson and Harry J. Snook.
The Macmillan Co.
$7.50 $6 \times 9\frac{1}{4}$; xiv + 659 *New York*

This stately and beautifully illustrated volume is intended to furnish those interested in natural history, whether professionally or as amateurs, with non-technical accounts of the structure and habits of the common seashore animals of the west coast of North America. The arrangement of the book is according to the taxonomic series. It covers only the invertebrates, with a short final chapter on the Chordata. It is very well done, and will have an even wider field of usefulness than that contemplated in its plan. There is a bibliography of 14 pages, a glossary, and a detailed index.

REPTILES AND AMPHIBIANS. *Their Habits and Adaptations.*
By Thomas Barbour. *Houghton Mifflin Co.*
$3.50 $5\frac{1}{2} \times 9$; xx + 125 *Boston*

This is a popular, but at the same time soundly scientific treatise on reptiles and amphibians, with special emphasis on their ecology, habits, and behavior. It is beautifully and extensively illustrated, contains a short selected bibliography, and is well indexed. It is an example of the highest type of popular natural history writing. A part of the material was used as a series of Lowell Lectures.

GENERAL CATALOGUE OF THE HEMIPTERA. *Fascicle I. Membracidae.*
By W. D. Funkhouser. *Smith College.*
$3.60 *Northampton, Mass.*
6×9; ix + 581 (paper)

This is the first part of an ambitious undertaking, which will be of great value

when completed to all entomologists, and particularly to hemipterologists. The general editor is Dr. G. Horváth, of the Museum at Budapest, and Prof. H. M. Parshley of Smith College is the managing editor. This first fascicle is devoted to the synonomy of the Membracidae, with indications as to the historical development of the knowledge of each species, and as to its geographical distribution.

THE PRACTICAL VALUE OF BIRDS.
By Junius Henderson. *The Macmillan Co.*
$2.50 $5\frac{1}{4} \times 7\frac{3}{4}$; xii + 342 *New York*

The author is the professor of natural history at the University of Colorado. The book is a detailed, fully documented presentation of the data of economic ornithology, based largely upon the examination of the stomach contents of North American birds. It is a valuable contribution to the literature of natural history.

TEXTBOOK OF GENERAL ZOOLOGY.
By Winterton C. Curtis and Mary J. Guthrie. *John Wiley and Sons, Inc.*
$3.75 $5\frac{3}{4} \times 9$; xv + 585 *New York*

An excellent textbook of elementary zoology, which "represents a temporary crystallization of the course in General Zoology as developed in the University of Missouri." From a pedagogical viewpoint it is sound, well-knit, and practical. We predict for it a great success in its field.

GLIMPSES OF ANIMAL LIFE.
By Various Authors. *John Murray*
2s. 6d. $4\frac{3}{4} \times 7\frac{1}{4}$; 184 *London*

A selection of quotations from the works of eight popular writers on natural history, the extracts being chosen "no less for the style" than for the information imparted. The result is a charming little book.

A LABORATORY COURSE IN GENERAL ZOÖLOGY. *A Guide to the Dissection and Comparative Study of Animals.*
By Henry S. Pratt. *Ginn and Co.*
$1.72 $5\frac{1}{2} \times 8\frac{1}{4}$; x + 244 *Boston*

This is a revised edition of the author's well known "Course in Invertebrate Zoölogy" with two vertebrate, perch and frog, discussions added in simplified form from his "Course in Vertebrate Zoölogy."

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 242. Methoden zur Untersuchung parasitischer Würmer. Züchtung parasitischer Würmer.*
By W. A. Collier. *Urban und Schwarzenberg*
2.50 marks 7 x 10; 42 (paper) *Berlin*

A useful summary of technique for the parasitologist.

BOTANY

A TREATISE ON THE BRITISH FRESH-WATER ALGAE.
By G. S. West. New and revised edition, in great part rewritten, by F. E. Fritsch.
The Macmillan Co.
$7.00 $5\frac{1}{2} \times 8\frac{1}{2}$; xv + 534 *New York*

This new edition of a standard systematic treatise on freshwater algae (and other pigmented Protophyta) will be found useful by all limnologists, and indeed general biologists. The revision has been thorough. There is much more extensive documentation of the literature than in the original edition. The keys for

the identification of the genera are excellently arranged. Sixty-two genera are included which were not in the earlier edition. Every British genus is figured. Altogether this is a valuable reference work.

NOTES SUR QUELQUES CAS DE TÉRATOLOGIE VÉGÉTALE. *Contributions du Laboratoire de Botanique de l'Université de Montréal, No. 6.*
By Frère Marie-Victorin.
University of Montreal
25 cents *Montreal*
6 x 9; 7 + 1 plate (paper)

NOTES POUR SERVIR À L'HISTOIRE DE NOS CONNAISSANCES SUR LES ABIÉTACÉES DU QUÉBEC. *Contributions du Laboratoire de Botanique de l'Université de Montréal, No. 7.*
By Frère Marie-Victorin.
University of Montreal
50 cents *Montreal*
6 x 9; 24 + 3 plates (paper)

NOUVELLES ÉTUDES SUR LES COMPOSÉES DU QUÉBEC. *Contributions du Laboratoire de l'Université de Montréal, No. 8.*
By Frère Marie-Victorin.
University of Montreal
50 cents *Montreal*
6 x 9; 20 + 4 plates (paper)

Interesting contributions respectively to teratology and morphogenesis; the history of Canadian botany; and local distribution and ecology.

PLANT ECOLOGY.
By W. B. McDougall. *Lea and Febiger*
$3.00 *Philadelphia*
$5\frac{1}{4}$ x $7\frac{3}{4}$; viii + 326

A well-written and extensively illustrated textbook for college and university classes in ecology. Each chapter is followed by a list of references for collateral reading, and at the end is a short chapter of suggestions to the teacher in arranging for laboratory and field work. An excellent text.

A TEXTBOOK OF BACTERIOLOGY. *A Treatise on the Application of Bacteriology and Immunology to the Etiology, Diagnosis, Specific Therapy and Prevention of Infectious Diseases, for Students and Practitioners of Medicine and Public Health.*
By Hans Zinsser (With a section on Pathogenic Protozoa, By E. E. Tyzzer).
D. Appleton and Co.
$7.50 6 x 9; xx + 1053 *New York*

The sixth edition, "rewritten, revised and reset" of a standard bacteriological text. The most important single alteration is a new section on parasitic protozoa by Prof. Tyzzer. In its new form this book will continue its long and deserved success.

THE BOTANY DRILL BOOK.
By H. G. Baker. *H. G. Baker*
Southwestern College, Winfield, Kans.
25 cents $3\frac{3}{4}$ x 6; 50 (paper)

A quiz compend, now in its second edition, containing 1000 questions and their answers, the latter consisting almost always of one word.

COTTON. *History, Species, Varieties, Morphology, Breeding, Culture, Diseases, Marketing, and Uses.*
By Harry Bates Brown.
McGraw-Hill Book Co., Inc.
$5.00 $6\frac{3}{4}$ x 9; xi + 517 *New York*

The scope of this agricultural text is sufficiently indicated in the sub-title. It is a thorough piece of work and a valuable addition to botanical and agricultural literature.

MORPHOLOGY

ANATOMICAL, PHYLOGENETICAL AND CLINICAL STUDIES ON THE CENTRAL NERVOUS SYSTEM.
By B. Brouwer. *Williams & Wilkins Co.*
$2.50 5½ x 8½; 67 *Baltimore*

These three lectures on the Herter Foundation, by the distinguished professor of clinical neurology at Amsterdam, deal respectively with (a) the projection of the retina in the brain; (b) the pathology of sensibility; and (c) the significance of phylogenetic studies for the neurologist. A bibliography of the pertinent literature follows each lecture.

VERTEBRATE EMBRYOLOGY.
By Waldo Shumway.
John Wiley and Sons, Inc.
$3.75 5¾ x 9; viii + 314 *New York*

A textbook of embryology for undergraduates. The forms particularly discussed are *Amphioxus*, the frog, the chick, and the pig. The first two parts of the book give a general account of development. The third and fourth parts are guides for laboratory work. The book is well illustrated, chiefly by clear line diagrams.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 236. Methoden zur Untersuchung der Morphologie der Primaten.*
By Stefanie Oppenheim, Adolf Remane, and Wilhelm Gieseler. *Urban und Schwarzenberg*
9 marks 7 x 10; 151 (paper) *Berlin*

An extremely useful handbook of directions for the quantitative study of the morphology, particularly skeletal, of the primates. Workers wishing to make biometric studies on any mammal will find it helpful, because it indicates clearly the measurements which will be comparable to those used in modern anthropometry.

HISTOLOGICAL TECHNIQUE. *A Guide for Use in a Laboratory Course in Histology.*
By B. F. Kingsbury and O. A. Johannsen.
John Wiley and Sons, Inc.
$2.25 5¾ x 9; vii + 142 *New York*

A useful laboratory guide, in which the first author contributes the vertebrate technique and the second, the invertebrate (particularly entomological). There is a bibliography of 54 titles.

PHYSIOLOGY

CONDITIONED REFLEXES. *An Investigation of the Physiological Activity of the Cerebral Cortex.*
By I. P. Pavlov. Translated and edited by G. V. Anrep. *Oxford University Press*
$9.00 6¼ x 9½; xv + 430 *New York*

This book is an English translation, by one of Pavlov's old students, of a series of 24 lectures delivered in Petrograd in 1924, which had for its purpose to summarize in a systematic way all of the work that had been done in Pavlov's laboratory on the activities of the cerebral hemispheres of the dog, which researches had been going on for more than a quarter of a century. It scarcely needs saying that it is a great and significant service to biology, on the part of both author and translator, to have made this most important work available in a more widely known language than Russian. There is no attempt to review the literature outside of that from Pavlov's own laboratory.

The whole book is just a straightforward, single-tracked exposition of the results of a wisely planned research program, persistently and painstakingly followed through. It is a pity that there are not more books like this.

ASPECTS ACTUELS DE LA PHYSIOLOGIE DU MYOCARDE (*Première Série*). *L'onde d'excitation motrice, son origine, sa propagation, ses manifestations électriques.*
By Henri Fredericq
Les Presses Universitaires de France
40 francs 6 x 9¼; viii + 300 *Paris*

A thorough review of the physiology of heart muscle, documented with a bibliography of 779 titles. The material is discussed under the following heads: The origin and the conduction within the heart of the excitation and the contraction; autonomous rhythms of the heart; neurogenic and myogenic theories of automatism and intracardiac conduction; the electrocardiogram from a physiologic point of view; the nature of the auricular and the ventricular systoles.

THE PHYSIOLOGY OF REPRODUCTION IN THE COW.
By John Hammond. *The Macmillan Co.*
$7.00 7 x 10; xvi + 226 *New York*

An interesting and valuable summary of the present state of knowledge of the physiology of reproduction and development of the udder in the cow, which includes a large amount of original data derived from the author's own investigations in these fields. It will be a first-order reference book for all students of agricultural physiology. There is a bibliography of 400 titles. The book is abundantly and beautifully illustrated, though in some cases, as for example Plate XX, the original photographic work could have been better done.

DIE UNREGELMÄSSIGE HERZTÄTIGKEIT.
By K. F. Wenckebach and Hch. Winterberg.
Wilhelm Engelmann
Leipzig
78 marks
Textband; 7 x 10; vii + 635
Tafelband; 7 x 10; 184 plates

This book started, in 1914, as a second edition of Wenckebach's treatise on the pathological physiology of the heart, but it was decided as the work progressed to rewrite practically the whole and make essentially a new work of it. In its new form it will constitute a basic reference work for the clinician and the student of pathological physiology. It is beautifully printed and illustrated. There is a bibliography of 1084 titles.

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome VII. Sang et lymphe. Réactions d'Immunité.*
By Ch. Achard, A. Besredka, Léon Binet, J. Besançon, J. Bordet, L. Cuénot, H. Delaunay, M. Doyon, R. Fabre, J. Jolly, Ph. Pagniez, G. H. Roger, F. Schulmann and P. Émile-Weil.
Masson et Cie
65 francs 6½ x 9½; xi + 502 *Paris*

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome XI. Reproduction.*
By Léon Binet, H. Busquet, Ch. Champy, E. Lesné, A. Pézard, Ch. Porcher, E. Rabaud, H. Vignes.
Masson et Cie
65 francs 6½ x 9½; xi + 496 *Paris*

These parts of the eleven volume text book of physiology which is being pro-

duced by the cooperation of the leading French physiologists and general biologists will be found useful for reference by American workers, chiefly because they reflect so thoroughly the French literature and point of view in the fields covered. The second of the two volumes here noticed has the greater general biological interest. Particularly noteworthy in it are the articles by Prof. Pézard on secondary sexual characters and by Prof. Porcher on milk secretion. The article on heredity by Prof. Rabaud will be regarded as reactionary by most American geneticists.

THE FOUNDATIONS OF NUTRITION.
By Mary Swartz Rose. *The Macmillan Co.*
$2.75 5 x 7½; xi + 501 *New York*

A popular book on diet, by the professor of nutrition at Teachers College, Columbia University, intended for "those who wish to live more intelligently." It is fully and rather well illustrated, and carries reference lists of literature after each chapter. Its viewpoint reflects that of the Columbia school of nutrition.

POTASSIUM AND TARTRATES. *A Review of the Literature on Their Physiological Effects.*
By Ralph W. Webster (With a Digest and Bibliography of the Literature, by W. A. Brennan). *The Commonwealth Press*
$2.50 5 x 7½; 168 *Chicago*

This is essentially an annotated bibliography of selected papers on the biological effects of potassium salts and of tartrates. While nothing is overtly said about it, we suspect that the underlying purpose of this treatise is that of propaganda in the baking powder war now on between Battling Alum of Chicago, and The Cream of Tartar Kid of New York.

THE METABOLISM OF THE FASTING STEER. *Carnegie Institution of Washington Publication No. 377.*
By Francis G. Benedict and Ernest G. Ritzman
Carnegie Institution of Washington
$2.50 *Washington, D. C.*
6¾ x 10; viii + 246 (paper)

A detailed investigation of the metabolism chiefly of two steers, which were subjected at various intervals during two and one-half years to seven fasting periods of from 5 to 14 days in duration. The results are too manifold and detailed for brief summary here.

RECENT ADVANCES IN HAEMATOLOGY.
By A. Piney *P. Blakiston's Son and Co.*
$3.50 5¼ x 8; viii + 276 *Philadelphia*

A useful contribution to the "Recent Advances Series," but of greater interest to the medical man than to the general biologist. The chapter on "Haemorrhagic Diatheses" will interest the human geneticist.

LEITFADEN ZU TIERPHYSIOLOGISCHEN ÜBUNGEN.
By Paul Krüger. *Gebrüder Borntraeger*
M. 3 5½ x 8¾; viii + 92 *Berlin*

A laboratory guide for a course in general physiology, by the *a. o.* Professor of Zoology and Comparative Anatomy at the University of Berlin.

PERMEABILITÄTSSTUDIEN AN EINER ÜBERLEBENDEN MEMBRAN.
By Ernst Wertheimer.
Urban und Schwarzenberg
2.40 marks 7 x 10; 25 (paper) *Berlin*

An account of an interesting series of investigations on permeability, made with

the surviving skin of a frog's leg as the membrane. The brochure constitutes the second number in the new series of *Fortschritte der naturwissenschaftlichen Forschung* edited by Professor Abderhalden.

BIOCHEMISTRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 227.* Containing the following articles: *Unsere Methoden zur graphischen Bestimmung des Gesamtgaswechsels*, by J. G. Dusser de Barenne and G. C. E. Burger; *Die Bestimmung des Blutgaswechsels einzelner Organe*, by Friedrich Verzár; *Stoffwechselversuch am Menschen und am Hunde*, by Robert E. Mark.

Urban und Schwarzenberg
7.80 marks 7 x 10; 124 (paper) *Berlin*

Lieferung 234. Containing the following articles: *Diazotieren*, by Siegfried Edlbacher, and *Ätzalkalischmelze Nitrieren*, by Ernst Maschmann.

Urban und Schwarzenberg
10 marks 7 x 10; 185 (paper) *Berlin*

Lieferung 237. Alkylieren.
By Josef Halberkann.
Urban und Schwarzenberg
12 marks 7 x 10; 220 (paper) *Berlin*

Lieferung 240. Acylieren. Acetalieren.
By Josef Halberkann.
Urban und Schwarzenberg
16 marks 7 x 10; 276 (paper) *Berlin*

Lieferung 243. Containing the following articles: *Biochemische Methoden auf dem Gebiete der Pflanzenhygiene*, by Julius Stoklasa, and *Die Phytochemie als Hilfsmittel zur Lösung phylogenetischer Fragen*, by Hermann Thoms.

Urban und Schwarzenberg
7 marks 7 x 10; 132 (paper) *Berlin*

These numbers of the Abderhalden handbook deal with various aspects of pure and applied biochemistry, and maintain well the high standard set in previous parts. The last paper listed, by Thoms, has considerable general biological interest.

THE CLINICAL INTERPRETATION OF BLOOD CHEMISTRY.
By Robert A. Kilduffe. *Lea and Febiger*
$2.50 $5\frac{1}{4}$ x $7\frac{3}{4}$; x + 186 *Philadelphia*

The purpose of this book is to furnish the practising physician with the necessary background to enable him to understand the significance of the findings of the laboratory man regarding the blood chemistry of his patients, particularly diabetics and nephritics. The compiling and editing are well done.

DIGEST OF ELEMENTARY CHEMISTRY.
By Martin Mendel. *Globe Book Co.*
67c 5 x $7\frac{1}{4}$; v + 234 *New York*

A quiz compend of chemistry for high school students.

LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE. *In 75 Vorlesungen, für Studierende, Ärzte, Biologen und Chemiker. II. Band: Stoffwechsellehre. IV. Lieferung: Eiweissstoffwechsel. Vorlesung: XLI Bis LI.*
By Otto Fürth. *F. C. W. Vogel*
Marks 15 *Leipzig*
7 x 10; iv + 148 (paper)

The topics treated in this part of the Fürth textbook of physiological chemistry, already noticed in THE QUARTERLY REVIEW OF BIOLOGY, are: Introduction to the theory of metabolism; protein diges-

tion in the stomach; protein digestion in the intestine; protein synthesis in the organism; proteolytic and peptolytic ferments; uric acid; hippuric acid; creatin and creatinin; oxyproteic acids; the fate of cyclic complexes of the protein molecule in the organism; haemoglobin excretion.

SEX

THE WOMAN A MAN MARRIES
By Victor C. Pedersen. *George H. Doran Co.*
$3.00 $5\frac{3}{4} \times 8\frac{1}{2}$; x + 276 *New York*

This is a realistic and mostly sound discussion of sex relations in married life by a physician. The point of view is to

> "treat of ignorance of biology and physiology, of social development and social conditions, of marriage, of venereal disease, and of the restoration or relief of the whole complex difficulty as fully as possible and as minutely as is wise for the purpose. Despite research and reading for many years in this field, I know of no other work which examines or aims to examine the relation of the so-called virtuous woman to the whole sexual problem. Very few persons in my experience, though careful thinkers, realize that women with misguided impressions of sex really live according to a double standard which is equally destructive of social and moral stability as the man's double standard. The effect of their double standard is that soon rather than late, and in high rather than low degree, they violate the marriage contract, because they enter into it under the pretense of normal, complete love and then reveal themselves as bereft of natural physical attachment without which the whole marriage soon disintegrates. The single standard for woman is to decide *before* marriage that *all* its obligations are acceptable to her and then proceed to live happily with her husband according to them. Like all other contracts marriage does not permit 'change of mind.'"

The author is opposed to birth control, except for certain definite medical reasons. At the same time the book has much to commend it.

LOVE AND MORALITY. *An Attempt at a Physiological Interpretation of Human Thought.*
By Jacques Fischer. *Alfred A. Knopf, Inc.*
$3.50 $5\frac{1}{2} \times 8$, x + 291 *New York*

A strange speculation, which starts by elaborating the thesis that the combined lipoids of the brain provide the causal basis and mechanism for its intellectual activities, and ends with a biochemical defense of homosexuality. In between is a lot about sex and morality and some biochemistry. The book is certainly original and is well-written, but the central thesis of it all wants a great deal more evidence in its support than can now be adduced, before the author's wide-ranging deductions can be taken seriously.

BIOMETRY

MATHEMATICAL STATISTICS. *The Carus Mathematical Monographs No. 3.*
By Henry Lewis Rietz.
Open Court Publishing Co.
$2.00 $5 \times 7\frac{5}{8}$; xi + 181 *Chicago*

An excellent little treatise, which puts its emphasis on the underlying mathematical theory of modern statistical methods rather more heavily than upon the practical applications and computations. It will, on this account, serve as a useful supplement to the elementary statistical manuals now in use.

A FIRST COURSE IN STATISTICAL METHOD.
By G. Irving Gavett.
McGraw-Hill Book Co., Inc.
$3.50 $5\frac{3}{4} \times 9$; vii + 358 *New York*

An elementary textbook of statistics along conventional lines. Four appen-

dices deal with elementary mathematics. There is little that is original in the book. The sources cited are to a large extent second-hand. Mr. Yule's middle name appears as "Udney" throughout the book.

THE QUANTITATIVE METHOD IN BIOLOGY.
By Julius MacLeod.
Longmans, Green and Co.
\$6.00 $5\frac{3}{8} \times 8\frac{3}{4}$; xxiii + 228 *New York*

The second edition of an original and stimulating treatise, which discusses quantitative biology along quite unconventional lines. The biometrician will profit by reading this book, not for technique but for ideas.

PSYCHOLOGY AND BEHAVIOR

THE CASE FOR AND AGAINST PSYCHICAL BELIEF.
Edited by Carl Murchison.
Clark University
\$3.75 6 x 9; 365 *Worcester, Mass.*

This is an entertaining book. Four kinds of people contribute to it. These are:

I. Those who are said to be "convinced of the multiplicity of psychical phenomena," which we take to be a hedging, professorial way of designating the worthy folk who swallow their spirits neat, raw, and without reservations as to time, place, or quantity. Here are found those doughty knights, Sir Oliver and Sir Arthur, and four others including, we blush to say, two ♀♀.

II. Those "convinced of the rarity of genuine psychical phenomena." Here are found McDougall, Driesch, Walter Franklin Prince, and F. C. S. Schiller. They like their spirits but are still moderate drinkers—the sort who claim to be able to "take it or leave it alone."

III. Those "unconvinced as yet." This has an ominous sound. The goblins will probably get them. There are two of these: John E. Coover and Gardner Murphy.

Finally, IV, are two staunch teetotallers, lips-that-touch-spirits-shall-never-touch-mine boys, who are "antagonistic to the claims that such phenomena occur." These two, of whom every scientific man should be proud, whether they are right or wrong, are Joseph Jastrow and the late, and greatly lamented, Harry Houdini.

The book is great fun, and the Clark University Psychology Department is to be congratulated for having staged so good a show.

SOCIAL PSYCHOLOGY INTERPRETED.
By Jesse William Sprowls.
The Williams & Wilkins Co.
\$4.00 $5\frac{3}{4} \times 8\frac{1}{2}$; xii + 268 *Baltimore*

This is a textbook for beginning students, written in the traditional mode of such books. The different theories of those who have discussed social psychology are expounded, charted in neat tables, and weighed against each other. But the "little red thread" is a very tenuous one indeed. About the only one we could find was that the author throughout regards it as impossible for individual behavior to be specifically distinguished from social behavior. It seems odd to find a book about social psychology in which neither Pareto nor Malinowski are mentioned, and in which there is no reference to William Graham Sumner's *Folkways*.

TIERSOZIOLOGIE. *Forschungen zur Völkerpsychologie und Soziologie, Band I.*
By Friedrich Alverdes. *C. L. Hirschfeld*
Mk. 4. 80 $6\frac{1}{4} \times 9\frac{1}{2}$; viii + 152 *Leipzig*
(paper)

This interesting volume fittingly opens a new series on folk psychology and sociology. The first four chapters are general discussions of animal associations; the reproduction of solitary animals; and social instincts in solitary animals. There then follows a long chapter giving the details regarding animal societies. With these data in hand the author proceeds to a general discussion of animal sociology and social psychology. There is a final short chapter on human social biology. There is a bibliography of four pages and an index. Altogether this is a useful addition to the literature.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

1st Book: THE ELECTRO-CHEMICAL FACTOR IN NEUROLOGY. *A Research in Electro Biology,* by *Ernest H. Pasqué.*
2nd Book: NEW CONCEPTS OF PHYSICS, *by Calvin S. Page.*
The Atomic Research Assoc.
\$10.00 $5\frac{3}{4} \times 9$; 604 *Detroit*

The chief conclusions of the first of these two books bound together are:

"In a general résumé of the facts as compiled in this work, we can say this: The energy recognized as solar and planetary electro-magnetic force, under specific conditions, combines atoms according to definite laws, into combinations of molecules, protoplasms, and nuclei, which form the combinations known as cells.

"These cells, by reason of their atomic (chemic difference between nucleus and protoplasm) have in themselves opposite polarity. The prevailing electro-magnetic environment of the moment is the selector, or determining factor of such original combinations; this establishes cell pattern. Each pattern possessing its own atomic individuality, thus giving the cell its selective properties, which is the basis of its future development. The opposite polarity or potential difference, with electro-magnetic energy as the external exitor factor, causes the cells to generate sufficient electric energy to enable them to absorb new atomic combinations of such quantity and kind as they require to maintain, or increase this potential difference in order to sustain themselves or multiply."

"Life is an electrical phenomenon. The body as a whole, and its different organs, are power stations for specific work, and the nerves like wires, form a complicated, yet efficient network of communication between these organs. This network of communication is again equipped with sub-power stations, condensers, or tuners, to check, block, release, increase or transform the electricity flowing through them, and operating the motors of such organs as are concerned in the vital generating process."

The second book is about "Rx The Life Atom."

"Rx is the newly discovered kind of atomic matter whose atoms repel each other, upon contact, by their inherent, repulsion Energy.

"Rx is of all colors, governed by the associated atoms, and is not affected by the force of gravity as are all other known atoms. Hence Rx matter has no weight.

"The atoms of each kind of matter cohere to Rx atoms only, upon contact, by their own strength of inherent cohesion Energy."

Rx is held to have great therapeutic significance. Just what it will do and how it will do it seem a little vague, but there is an abundance of assertion that it will. On page 569 (near the end of the book) we find the following statement, which ought to be reassuring.

"Hence with this knowledge of Rx in the essential functions of organic nature it is self-evident that there must be great therapeutic value in the scientific application of light to the human body. I say scientific because the wonderful refinement of the harmonious operations of the cycles of animal life is not only evident in perfect health but in the universal constancy of the temperature of 98.6°."

STANDARD METHODS OF THE DIVISION OF LABORATORIES AND RESEARCH OF THE NEW YORK STATE DEPARTMENT OF HEALTH. *General Laboratory Procedures and the Methods Used in the Department for the Preparation of Media and Glassware; the Laboratories for Sanitary and Analytical Chemistry; the Research, Publications, and Library Department; the Antitoxin, Serum, and Vaccine Laboratories; the Diagnostic Laboratories; the Executive Offices.*
By Augustus B. Wadsworth.
The Williams & Wilkins Co.
$7.50 6 x 9; xx + 704 *Baltimore*

Dr. Wadsworth's laboratory in Albany is deservedly regarded as a model which marks the way of advance in public health laboratory work. It is a great service to have brought together in one volume a clear and detailed account of the organization of the Division of Laboratories and Research of the New York State Department of Health, and of the methods there used. This book will at once take rank as the standard reference work on laboratory technique for public health departments.

THE LION-HEARTED KITTEN *and other Stories.*
By Peggy Bacon. *The Macmillan Co.*
$2.00 $5\frac{1}{2}$ x $8\frac{1}{2}$; 102 *New York*

This is an entertaining contribution to the Higher Biology. The drawings are superb. The tales which go with them are not quite so distinguished, but still there are high points, as, for example, the solemn discussion between the giraffe and the woodpecker, who had mistaken the former's neck for a tree trunk, as to whether the giraffe *was* a tree or not. This is a book to be read aloud in every biologist's home circle. It is suited to all ages.

ACUTE RHEUMATISM IN CHILDREN IN ITS RELATION TO HEART DISEASE. *Reports on Public Health and Medical Subjects No. 44.*
Ministry of Health.
H. M. Stationery Office
1s 6d. $6\frac{1}{8}$ x $9\frac{3}{4}$; xii + 99 *London*

This is a report of a study by several officers of the British Ministry of Health on the bacteriology, incidence, and institutional treatment of acute rheumatism in children, considered in relation to the prevention of heart disease. It is a thorough piece of work of great interest to the student and the practitioner in the public health field.

INTRODUCTION TO THE HISTORY OF SCIENCE. *Vol. I. From Homer to Omar Khayyam. Carnegie Institution of Washington Publication No. 376.*
By George Sarton.
The Williams & Wilkins Co.
$10.00 7 x 10; xi + 839 *Baltimore*

The reputation of George Sarton in the field of the history of science has been firmly established by his journal *Isis.* We now have the first volume of what must for a long time be the master-work in the history of science, if it is completed along the lines laid down in this beginning. The ordinary man would be overwhelmed by the colossal nature of the task outlined. But Dr. Sarton cheerfully contemplates the preparation of *six more* volumes, each of the order of this one, as necessary to lay the *preliminary* foundations upon which alone a sound history of science may be written! May God spare him for his labor! For it is good. The present volume covers the period from Homer to Omar Khayyam, that is to say

up to the end of the eleventh century. The book is essentially an enormously thorough, detailed, and erudite bibliography, with pertinent and penetrating annotations. The subject is conceived so broadly that it will serve about equally well for a source book on the history of civilization, as on the history of science.

VOL. III, NO. 2 JUNE, 1928

THE QUARTERLY REVIEW of BIOLOGY

HOMOLOGY, ANALOGY AND PLASIS

BY JOHN TAIT

Department of Physiology and Experimental Medicine, McGill University

IN THE days of Spallanzani and of John Hunter comparative anatomists did not scruple to employ experimental means as an aid to investigation. In their time no hard and fast distinction had been made between questions pertaining to structure and questions pertaining to function. Function and structure being viewed as more or less of a unity, biologists felt free to employ any available means in the investigation of their multifarious problems. In the process of historical development physiology hived off from anatomy and very soon two distinct sciences, each employing its own special technique and animated by its own particular aims, had replaced the more generalised biology of Hunter. During the nineteenth century the separation between them became profound. Of recent years we have witnessed a strong tendency on the part of zoologists and anatomists to recur to the experimental method. It began with Darwin and to a less degree with Milne Edwards. It received a very strong impulse in a special direction from Wilhelm Roux and in another direction from Gregor Mendel. More particularly in America, where a strong group of men, prepared in Johns Hopkins University by the joint labors of Brooks and of Newell Martin, were ready at an opportune moment to develop and greatly to extend the biology of Roux and of Mendel, zoology is now viewed as an experimental rather than as a comparative science. In process of time no doubt matters will readjust themselves and the comparative method of studying structure will again come more into vogue. When it does it too will have to be handled experimentally.

As physiologists are not generally aware of the opportunity open to them of participating in some of the classical problems of comparative anatomy, and as the morphology of our fathers has for the moment fallen on evil days, it seemed worth while to go over the history of the original separation between physiology and comparative anatomy with a view to make some constructive attempt towards a *rapprochement* between them. The whole issue is rather a wide one and cannot well

be covered in a short article, but the matter may be partially handled by discussing afresh the vexed question of homology and analogy. The line of treatment here presented, of necessity somewhat formal, owes its origin to a suggestive communication by Keith Lucas on *The Evolution of Animal Function*—cf. also E. S. Russell (1916) and Tait (1917,a). Lucas correctly traced the ultimate complete separation between physiology and comparative anatomy to the outcome of the famous discussion that arose between Cuvier and Geoffroy St. Hilaire as to the criteria of comparison of animals for purposes of classification. In this discussion, as we know, Geoffroy prevailed over Cuvier.

HOMOLOGY AND ANALOGY

Let us go back to the time of Cuvier and Geoffroy. Many of the characteristic parts of animals, head, eyes, legs, wings, etc., had long received at the hands of mankind distinctive names indicating equivalence or correspondence. A child can scarcely fail to recognize the essential similarity between, say, the legs of a fly and the legs of a cat. The comparative anatomists, having recognized a certain number of different types or patterns of bodily structure, were now faced with a difficulty of a novel nature. An insect and a bird—to select a particular pair of animal forms—belong to two different types of organization. In what sense are the wings and the legs of the insect equivalent to those of the bird? The penetrating mind of Geoffroy St. Hilaire seized upon a way out of this difficulty. The wings of the insect resemble those of the bird only in so far as they subserve the same function. Though the bird, in virtue of its power of flight, may seem to occupy an anomalous position in the vertebrate series, in essential structure it thoroughly conforms to type, and comparison shows that the bird's wing is, from a structural point of view, the equivalent of the fore-limb of any other land vertebrate. The insect's wing, which is not a modified limb, is obviously a different article.

The conclusion was that, for a decision on questions pertaining to the arrangement or classification of animals, we should close our eyes to similarities dependent on mere equivalence of function, and concentrate solely upon intrinsic structural features. Owen later codified the terminology by which these two forms of resemblance are distinguished. Parts or organs of one animal which have the same function as parts or organs in a different animal he termed *analogous*. Parts or organs structurally identical under every variety of external form and of function he termed *homologous*. Biologists thereupon decided to discount analogies, the determination of homologies being considered as rendering better service for their purpose.

The introduction of this distinction between analogy and homology, valuable and indispensable as it was for its special purpose, reacted upon the outlook of physiologists and of anatomists alike. It appeared as if a verdict had been pronounced against the right of physiology to participate in the larger problems of structure, and the effect was to produce a disunion of effort between the two colleagues in what had previously been considered common, or at least closely contiguous, territory. Medical demands being urgent, the physiologists fell back almost entirely upon study of the mechanism of the human body, and it is curious to note how their science remained thereafter unresponsive to and untouched by some of the broader and more liberal developments of biological investigation,

developments with which comparative anatomy continued in complete rapport.

The adjective *homologous* is in reality a geometrical term and applies to corresponding members of similar figures. For example, in the two similar pentagons $\alpha\,\beta\,\gamma\,\delta\,\epsilon$ and *ABCDE* the line $\alpha\,\gamma$ is homologous with the line *AC*. So too are the sides $\alpha\,\beta$ and *AB*, $\beta\gamma$ and *BC*, $\gamma\delta$ and *CD*, respectively homologous. In "ideal" morphology the use of the word "homologous" in this positional sense is appropriate and serves a useful purpose. It condenses into one phrase Geoffroy St. Hilaire's famous *principle of connexions*, according to which parts are comparable when they occupy corresponding positions, i.e., have identical spatial relations, in the organisms selected for comparison.

Owen's definition of analogy is: "A part or organ in one animal which has the same function as another part or organ in a different animal." Now, in text-books of comparative anatomy we find that it is customary to analyze animals into systems of organs, thus:

Integumentary,
Skeletal,
Muscular,
Alimentary,
Excretory,
Circulatory,
Respiratory,
Nervous,
Sense Organs,
Reproductive,
Endocrine.

The original conception of this device is due to Cuvier, and it will be noted that the names of these systems, which recur almost en bloc in different phyla, are predominantly functional in signification. Systems, however, are made up of "parts or organs," and as modern comparative anatomists are only too well aware, the fact of analogical resemblance between organs is in itself a thing of extreme interest—cf. Willey. The exponents of ideal morphology discarded likenesses of analogy for two reasons: (1) they elected to believe that structure is prior to and determines function, or, as Geoffroy St. Hilaire put it, "animals have no habits but those that result from the structure of their organs; if the latter varies, there vary in the same manner all their springs of action, all their faculties and all their actions;" (2) equivalence in the matter of spatial relationships, being a more precise conception than "functional" equivalence, could be forthwith applied as a criterion of comparison.

THE QUESTION OF FUNCTIONAL EQUIVALENCE

Let us consider for a moment some of the complications involved in so-called functional equivalence.

The difficulty of precise definition. For simplicity let us begin with a concrete example. Let us take an obvious action, such as that of a wing, which is used for flying. How do we define flight? Flight involves in the first instance progression through the *air*, but so does a mere fall as well as a leap. We therefore incorporate as an essential element the idea of *support* by the air itself. So modified, the definition still includes the drifting of a balloon. We rectify once more and impose the condition that the flying body must be *heavier than air*. Soaring and parachuting have still to be eliminated. We amend again and stipulate that *the energy determining the progression must not be derived from movement of the air itself*. With it all we have yet failed to eliminate gliding, as from a precipice or other attained height. So we lay down the further condition that *the energy involved shall not necessarily have been imparted before launching into the air.* With these several stipulations we finally conclude that the flying body, itself heavier than air, must be a source of energy

and that this energy is used simultaneously for its support and for its forward progression, in virtue of the reaction or inertia of the air. So defined, flight would include the flight of a bird or of an insect, of a flying machine, of a rocket and of an aerial torpedo, but not of a flying fish, of a pterodactyl or of a flying phalanger. To one whose pursuits have lain chiefly in the field of comparative anatomy such analysis may appear fussy and beside the point, particularly in its invocation of energy considerations, and that to the exclusion of the wing itself. To the student of function this mode of procedure is a *sine qua non;* it is his comparative method; in which respect our cited case is merely an example of a general and invariable mode of attack. With advance of time, too, the elaboration of specification tends to increase, and even our example involves elements that are novel since the time of Cuvier and Geoffroy. Similar analysis is involved in terms like walking, running, swimming, breathing, feeding, excreting, etc. When we say that a system of organs, or even a particular part, subserves a certain use or function, it is necessary, in order to avoid confusion, to be scrupulously explicit. As a very simple illustration let one consider the fundamental difference between feeding of a Paramecium, which ingests food particles bodily into its protoplasm, and the corresponding process in higher animals, which first reduce their food to a soluble condition before absorption.

The two meanings of "function." Another, and more vital, complication is that the word function is ordinarily employed in two quite distinct senses: (1) to indicate the general *use* or application of an organ, as in the phrase "to subserve a function"—the cases already cited come under this category; (2) to cover the individual events or interior processes which go on in its constituent cells, i.e., the essential or intrinsic physiological mechanism of the part. Modern physiology has concerned itself particularly with function in the second sense, which we may here for convenience call "Function *B*," whereas Geoffroy St. Hilaire and Owen, in their institution of the conception of analogy, were thinking only of the first, which we may call by the name of "Function *A*." Thus it is that a physiologist of the present day, suddenly confronted with Owen's definition of homology and of analogy, is at a loss to understand from the examples cited by way of illustration wherein the averred distinction lies. He instinctively looks for a difference in essential mechanism, let us say, between legs, wings and fins, and finds none. To him all these appendages are simply pegs or bone-linkages moved in an adequately coördinated fashion by muscles under the domination of the central nervous system—cf. Keith Lucas.

Similar use but different intrinsic mechanism. On the other hand—and this involves a third complication—it has been found that organs which fulfil equivalent requirements so far as the needs of the animal are concerned, may differ in intrinsic physiological mechanism. Thus, the heart of a mammal and the heart of the king-crab *Limulus* perform in each case the office of pumping the blood. The muscle of the mammalian heart, however, exhibits a marked refractory phase after each beat, cannot be held in continued contraction by serial stimulation and has inherent rhythmic power, whereas the muscle of the heart of *Limulus* has no enduring refractory phase, can by a series of stimuli be maintained in steady contraction and ceases to beat when separated from the central nervous system (Carlson). To Geoffroy St. Hilaire and to Owen these hearts, which prove on

experimental investigation to be so dissimilar, would doubtless have appeared as functionally equivalent just because both subserve the same use.

As another example one might adduce those types of articulation which in certain animals permit not only of free hinge movement in various directions but also of torsional movements. In vertebrates these are the ball and socket joints. An articulation permitting similar freedom of movement is the coxo-basal articulation of isopods (Tait, 1917,b). The design of this joint is quite different from that of the bony ball and socket. The hollow cylinder of the basipodite rests by its edge upon a projecting hook-like process of the coxa. Another device designed to give similar results is that present in the Balanidae (Tait and Emmons). The operculum of these sessile cirripedes does not articulate at any fixed point directly with the surrounding shell. It rests upon a closed cushion of fluid, and is bent in any given direction or torsionally rotated by means of appropriate muscles, the underlying fluid being meantime subjected to high pressure. In these various articulations, therefore, we find three different types of physical or physiological mechanism, all designed to give the same complex result.

Indications are not wanting that equally striking differences in intrinsic mechanism exist between selected organs of one animal group and their accredited analogues in other groups.

By way of résumé we may note the following. In asserting a functional difference between organs, one must distinguish clearly between function in the sense of use (Function *A*), and function in the sense of intrinsic mechanism (Function *B*). In the historical separation of likeness by "analogy" from likeness by "homology," the use of a part (Function *A*) is what was meant by its function. It is particularly to be noted that neither Geoffroy St. Hilaire nor Owen established any case of homology in which function in the sense of intrinsic mechanism (Function *B*) varies; in all the subsequently accepted cases of homology suggested by them the essential mechanism remains unchanged. At the same time it is possible to point to deep-seated differences of function (i.e. Function *B*) in organs which they would undoubtedly have slumped together as analogous.

It is true that Geoffroy sought to develop a detailed homology between a skeletal segment of an arthropod and a vertebra of the Chordata. Von Baer, also on homological grounds, explained the conformation of a vertebrate as being a compound between articulate and molluscan elements, the animal parts (*sensu* Bichat) of the vertebrate being of the articulate type, the vegetative parts being of the molluscan type. These and many similar erroneous attempts at homological reasoning, perfectly valid according to Geoffroyian criteria, were seen to be grotesque so soon as the doctrine of likeness by descent became prevalent; but it may also be pointed out that such cases of fictitious homology would equally have broken down if tested by the criterion of function in the sense of intrinsic mechanism (Function *B*).

OWEN'S "ANALOGY" NOT A PURELY FUNCTIONAL CONCEPTION

In view of an occasional misconception it is well to bear in mind that though Owen's definition of analogy is phrased in purely functional terms, it nevertheless bears an inherent structural connotation. We might illustrate by reference to the so-called reticulo-endothelial system. When foreign particles are injected into the circulation of a mammal they come to

rest in three several organs, viz. the spleen, the liver and the bone marrow. Microscopic examination shows that in these sites the normal vascular endothelium is wanting, and that the particles have been ingested by special cells, the Kupffer cells of the liver, the cells of the splenic ellipsoids and other special cells of the marrow. Now, in accordance with the literal terms of Owen's definition it might be stated that these phagocytic vessel-lining cells, which all react in the same way towards particles, are "analogous" elements.

It should be kept in mind, however, that the original purpose of the definition of analogy was not to serve a physiological end, but to prevent confusion in a structural inquiry. The analogous organs of interest to Geoffroy St. Hilaire were, for example, the legs or arms of arthropods, of cephalopods and of vertebrates; the wings of insects, of birds and of bats; the valves of Cirripedia, of brachiopods and of acephalous molluscs; the tail-parts of arthropods and of vertebrates; the tentacles or antennae respectively of gastropod molluscs and of arthropods—in each case structures which to the laity might appear identical, but whose fundamental structural inequivalence is for the first time revealed by comparative anatomy. While Owen's definition of analogy was so phrased as not to include any formal reference to structure, the context sufficiently shows that it carried a structural connotation, being designed to anticipate the very blunder that on a superficial view might cause embarrassment. Introduced as a complementary term to homology, for use in purely structural inquiries, it was originally aimed at organs which in virtue of similar environment show an external structural correspondence. On its first introduction therefore the word analogy had no exclusively functional meaning, contrary to what some modern writers occasionally assume. Essentially it involved a structural connotation, and the real truth is that Geoffroy and Owen, in setting up analogy against homology, were struggling to formulate a distinction between what we should now prefer to call similarity by convergence and similarity by descent.

THE EMBRYOLOGICAL OR GENETIC CRITERION OF HOMOLOGY

With the advent of Darwinism a curious thing happened in regard to the criteria of homology. Structural likenesses being seen to depend, not on unity of plan, but on descent from common ancestors, the original geometrical conception of homology, which for the sake of distinctness we might now call "positional homology," was allowed quietly to lapse. One might suppose that the term homology, having outlived its *raison d'être*, would ultimately have died out. Instead, it adapted itself to its new surroundings and emerged in a new guise and with transformed meaning, which we shall here designate as "embryological homology." The change of meaning of the word, which we have indicated by prefixing to it special adjectives, occurred so easily and so naturally that for a time the matter escaped analytical inquiry.

Fritz Müller was early in the field with support for Darwin's theory of descent. Müller's main contention was that during the development of various animals, especially the Crustacea, the embryos pass through successive stages which resemble the presumable line of historical descent of the adults. Haeckel, seizing upon this conception, which he extended with a wealth of illustration to the animal kingdom at large, gave it concise form in his statement of the so-called "biogenetic

law," according to which the ontogenetic development exhibits an abbreviated repetition of phylogenetic history, in other words that individual embryonic stages represent reanimated but schematised ancestors of the fully developed animal. If now two apparently diverse organisms are found to be structurally comparable, part for part, in the adult stage, will not their individual homologies be rendered more evident by examination of their development (which, by hypothesis, mirrors their phylogeny) before specialisation or extreme differentiation has occurred? Particularly apposite evidence in support of this notion was already to hand from the science of embryology. Consequently we find Haeckel announcing that "true homology can only exist between two parts which have arisen from the same primitive 'Anlage' (embryonic representative) and have deviated from one another by differentiation only after the lapse of time."

For the moment the old positional or geometrical conception of homology had faded into the background. Gegenbaur's definition of special homology, viz., "the relationship between two organs which have had a common origin, and which, as a corollary, have arisen from the same Anlage," incorporates to the full the biogenetic law of Haeckel. The new interest attaching to the establishment of "homologies" was thus expressed by Gegenbaur: "Homology . . . . corresponds to the hypothetical genetic relationship. In the more or less clear homology, we have the expression of the more or less intimate degree of relationship. Blood-relationship becomes dubious exactly in proportion as the proof of homologies is uncertain."

How now does the amended criterion of homology work out in practice? For one thing the old bugbear of analogical resemblance or similarity by adaptation was not yet lightly to be exorcised, and we find Haeckel remarking: "In evaluation of anatomical resemblances . . . . everything in the last issue invariably depends on the decision whether the ultimate correspondences in structure are to be looked upon as homologies (maintained by common descent) or as analogies (acquired by similar adaptation). Important as it is, this very decision is often extremely difficult." Another perplexity inherent in the new definition was that which occurs to so many young students of morphology, namely, of fixing a limit of commencement to the "Anlage" of an adult organ; for a group of such "Anlagen" may have themselves a common "Anlage" in an earlier period of development; in this way one arrives at the blastomeres and finally at the ovum itself. Partly as a correction against this perfectly pertinent but perfectly useless extension of the embryological criterion—which, interpreted phylogenetically, would make almost all organs of any one phylum homologous one with another—and partly because of greater convenience in practice, the evolutionary morphologists, while introducing the embryological conception into their definition of homology, continued in the habit of establishing homologies by comparison of adults, just as the older anatomists did. It has ever proved more easy to alter a creed than to uproot long-established usages associated with an older faith. While the morphologists professed embryological homology, their conduct alternated between the homology that depends on simple position and that which is defined in terms of similarity of development.

If we inquire as to the place allotted to function in the new order of things, we find that it was consistently discussed in the sense of use or application (Function

A), just as of old. As an extreme illustration one might select Reichert's demonstration by embryological means of the homologies of the auditory ossicles of mammals, which proved to be a modification of the whole hinder portion of the lower jaw, as it exists in reptiles, as well as of the separate quadrate. The striking nature of this case leads Gaupp to remark: "Thus we have here in the history of the auditory ossicles of mammals a highly remarkable case of change of function, perhaps the most remarkable case in the whole realm of vertebrate morphology; skeletal parts which previously formed important members of the mandibular apparatus, are in the mammal alienated therefrom and assigned to an entirely new duty." In this particular instance, where a series of articulating bones commences and ends as a bone-linkage, it is almost unnecessary to point out that as a form of intrinsic physiological mechanism it remains almost the same. To this day the question has scarcely been raised whether identity in respect of Function *B* should not be incorporated as an essential element in our predication of likeness by homology.

HOMOGENY AND HOMOPLASY

As we have just seen, morphologists were not always careful to distinguish the homology based on comparison of adult characters from that which is embryologically determined. By injecting into positional homology all the implications of the theory of descent, they persuaded themselves that when they determined homologies after the old fashion, they were establishing embryological homology. In an important communication published in 1870 Ray Lankester drew attention to the danger of this procedure. In order to rectify matters he proposed at the same time a reform of the terminology, his statement being somewhat as follows:

He first suggested that organs may appropriately be called *homogenetic* if the common possessors are derived from ancestors that possessed the same organ. But homology had not infrequently been based upon considerations of pure position. Thus, the four cavities of the bird's heart had been said to be homologous with the four cavities of the mammalian heart, in spite of the fact that the common ancestors of mammals and birds had in all probability but three heart cavities, and in spite of the further fact that the right ventricle of a bird's heart does not develop in the same way as the right ventricle of a mammalian heart. Again, certain muscles in the limbs of Sauropsida were said to be homologous with other muscles in the limbs of Mammalia, although the presumption was that no such muscles were present in the limbs of the common amphibian ancestors. (Here Lankester was following Huxley's now discredited derivation of mammals from an amphibian and not from a reptilian stock.) "Again," says he, "it may perhaps be admitted that the common ancestors of the Osseous Fishes and Mammalia had a skull of decidedly undifferentiated character, with a much less amount of differentiation than is observed in the skulls of either of these groups. It is only in so far as they have parts represented in the common ancestor that we can trace *homogeny* in these groups; and yet the *homology* of a vast number of bones in the skull of the two is discussed and pointed out." He further instanced the serial homologies, in which a correspondence is traced in detail between the structures composing, say, the fore-limb and those composing the hind-limb of one of the higher vertebrates. His conclusion was that something over and above

simple *homogeny* is in such cases connected by the term homology, and he proceeded to state the proposition thus: "When identical or nearly similar forces, or environments, act on two or more parts of an organism which are exactly or nearly alike, the resulting modifications of the various parts will be exactly or nearly alike. Further, if, instead of similar parts in the same organism, we suppose the same forces to act on parts in two organisms, which parts are exactly or nearly alike and sometimes homogenetic, the resulting correspondences called forth in the several parts in the two organisms will be nearly or exactly alike. . . . . I propose to call this kind of agreement *homoplasis* or *homoplasy*. . . . . What is put forward here is this: that under the term 'homology', belonging to another philosophy, evolutionists have described and do describe two kinds of agreement—the one, now proposed to be called 'homogeny', depending simply on the inheritance of a common part; the other, proposed to be called 'homoplasy,' depending on a common action of evoking causes or moulding environments on such homogeneous parts, or on parts which for other reasons offer a likeness of material to begin with."

Lankester's paper is perhaps the most interesting *tour de force* in the history of the subject. We shall take up in order the questions it raises.

Homogeny. As already indicated, this is simply a distinctive name for embryological homology, so designed as to preclude any chance of misapplication or misapprehension. Because of its doubtful antecedents (note his phrase, "belonging to another philosophy"), he drops the word homology altogether.

Homoplasy. This conception, being a novel one, demands and obtains chief consideration in his paper. It has for us a two-fold interest: (1) in respect of the plasis or moulding idea; (2) in respect of the relation of homoplasy to the old analogy.

Plasis or moulding. Significant is his clear enunciation, at this early date, of the conception that (by whatever imaginable means) forces of environment act upon and mould developing structure. The language, be it observed, is not that of natural selection; actively determining or causal *forces* are predicated. Though the experimental procedure is lacking, his speech is essentially the speech of *Entwicklungsmechanik*, and to this extent foreshadows a new outlook.

Homoplasy and analogy. In view of what has preceded, we naturally ask: "In what regard, if any, does homoplasy differ from the old (structural) analogy?" Lankester did refer to the point in his paper, but elected, for reasons which he does not specify, to differentiate between the two. By confining the application of his term "homoplasy" to organisms or parts of organisms which are nearly or exactly alike, he seems deliberately to have limited its scope. Possibly, too, he was influenced by the feeling that the classical cases of analogy would presuppose forces of external environment, whereas in his illustrations of homoplasy the internal environment of the animal is apparently the main moulding influence.

In later life Lankester has shown a disposition to extend the scope of his homoplasy so as to cover all cases of convergence or parallelism. His original definition involved simultaneous specification of two separate likenesses, (1) "identical or nearly similar forces of environments," (2) "parts of an organism which are exactly or nearly alike," or "parts in two organisms, which parts are exactly or nearly alike," or "parts which for other reasons show a likeness of

material to begin with." For establishment of homoplasy, according to the definition, both conditions have to be satisfied. Condition (1) is phrased in sufficiently general terms to include external as well as internal environment. The main question that arises is the precise degree of restriction imposed by condition (2). In a reply to H. F. Osborn (1907) he says, "Can you imagine cases of convergence or parallelism which are not covered by the definition I gave of homoplasy? What organs are parallel in any two animals and yet have no likeness at all—even the most general—in their material?"

From these sentences it would appear that Lankester might have been willing to omit condition (2) from his definition. It must be kept in mind that in his original paper he did more than define homoplasy; he committed himself to a statement or proposition as to the action of similar environmental forces on two separate things, and, for the purpose of this proposition, condition (2) may have been necessary. When, however, close structural likeness is seen to arise between two very diverse things—likeness which is obviously correlated with, or rather dependent upon, identity of environment—it should be quite permissible to designate the resemblance as homoplasy. The various instances of analogy are just of this kind, e.g., the wings of bats, of birds and of insects; the eyes of Pecten, of cephalopods and of vertebrates; the otocysts of various invertebrates and their labyrinthine equivalents in vertebrates; the division of the body into leaves, stem and roots in the case of the higher plants (diploid generation) and of mosses (haploid generation); the hyphal form of parasites, such as the Fungi among lower plants, *Rafflesia* among higher plants, *Sacculina* among animals; the hold-fast organs (haptera) of seaweeds and green algae, perhaps the adhesive roots of ivy and adhesive stems of *Ampelopsis*, the adhesive base of certain unicellular animals (e.g., *Vorticella*), of sponges, of zoophytes, of sea anemones, of crinoids, of Cirripedia and of sessile tunicates. If this interpretation of Lankester's meaning be correct, then, as Osborn says in an amended statement, "Lankester's homoplasy is equivalent to analogous evolution, to parallelism, or convergence."

EXPERIMENTAL CONTRIBUTIONS TO HOMOPLASY

Just as Owen based the conception of analogy on morphological evidence, so it was by purely morphological testimony that Lankester was led to institute the idea of homoplasy. Of recent years physiology and experimental embryology have begun—in some cases almost unwittingly—to furnish evidence touching upon the question of homoplasy. With the help of some illustrative cases we may briefly indicate the significance of these experimental contributions to the subject.

Examples. It is well known that normal development of (1) the accessory sexual organs (e.g., the vagina, uterus, Fallopian tubes and mammary glands of the female, the vesiculae seminales and prostate gland of the male) and (2) of the so-called secondary sexual characters of mammals, is dependent upon the presence of the gonads. When the ovaries or the testes of a vertebrate are removed in youth, the growth and differentiation of the accessory sexual organs is faulty and the secondary sexual characters are absent. By grafting into the castrated animal a gonad taken from another animal of similar species and sex, the defective organs or characters are induced to resume development. Experiment has shown

that the effective part of the gonad, in the case of the male at least, is, not the spermatogenic tissue, but the interstitial cells or so-called "interstitial gland." Obviously the Anlage or embryonic representative of, say, the prostate gland of the young male animal does not of itself possess the power of developing to completion; for the attainment of full structural maturity a "hormone" derived from the interstitial gland is necessary.

In most cases of development no such correlation of separate parts (one primary, the other secondary) has as yet been verified. At an early and quite undifferentiated stage of development of the respective parts, Braus removed the little outgrowth or bud which represents the hind-limb of a tadpole and inserted upon the wound of the trunk thus caused the bud of a fore-limb. In its abnormal situation the latter grew and developed into a typical and full-sized fore-limb, in which not only the various bones, muscles, joints and ligaments were complete, but in which the orientation of the mature transplant, as regards preaxial and postaxial borders, depended upon the original orientation of the graft. In this case, selected as a type of the usual experimental finding, the Anlage possesses the power of "self-differentiation," to use the language of Roux—that is to say, it grows and continues to unfold by its own inherent impulse. In the development of the prostate gland, on the other hand, we have a case of "dependent differentiation," in which the power of unfolding to completion does not wholly reside within the Anlage. In the differentiation of the prostate a moulding influence, specifically hormonic and external to the organ itself, comes into play.

In respect of the secondary sexual characters, castration, whether of a male or of a female vertebrate, produces a common "neutral" or "indifferent" type of animal, and Steinach has shown that by experimental interchange of gonads it is possible to "masculinize" an originally female and to "feminize" an originally male animal. Thus castration and implantation of an ovary into a male guinea-pig lead to marked growth and differentiation of the mammary glands, while implantation of a testis into a spayed female leads to a penile enlargement of the clitoris. Lipschütz (1919) in a special investigation of the last-mentioned change finds that corpora cavernosa make their appearance in the clitoris of the inverted guinea-pig and also special horny spikes characteristic of the guinea-pig penis. In the formation of these corpora cavernosa and horny spikes we have an experimental case of moulding by the environment, for in the absence of the hormone from the male interstitial gland they do not develop, the clitoris remaining a clitoris. As establishing actual homoplasy with the corresponding structures of the male penis, Lipschütz (1924) has also shown that the development of the horny spikes in the penis of a male guinea-pig depends upon the testicular hormone.

Other cases of homoplasy have also been induced experimentally. In the development of the vertebrate eye it has long been known that the essential parts arise from two separate Anlagen; the light-recipient apparatus or retina as a hollow protrusion of the brain, which, becoming invaginated, forms the optic vesicle; the main light-refracting apparatus or lens as an ingrowth of the skin. The development of the optic vesicle proceeds by self-differentiation; when it is dissociated from any connection with the brain it forms a complete retina (W. H. Lewis, Spemann). The development of the lens is a case of dependent differentiation; in the absence of the optic vesicle it fails to

differentiate. If in a larval amphibian the skin overlying the optic vesicle is removed and replaced by skin from any other part of the body, a perfect lens is formed by the transplanted skin (W. H. Lewis). Furthermore an optic vesicle, grafted into an abnormal site, proceeds to modify the overlying skin so that it becomes a lens. In this case the influence exerted at close range by the optic vesicle upon the indifferent skin tissue is not simply that of a chemical messenger or hormone; something more suggestive of physical moulding must come into play, otherwise it is hard to conceive how the proper amount of (indifferent) tissue is selected and adjusted to fit the mouth of the vesicle.

While we have merely touched on the fringe of this more modern line of investigation, the instances given suffice to show that the moulding influence of the internal environment of an Anlage that is not self-differentiating has been brought within the scope of experimental study. In our selected cases the decisive influence exerted upon the non-self-differentiating Anlage has been proved to have its seat in one single primary or controlling organ (or Anlage), to which the other is secondary or subservient—in which respect Lankester's supposition of plasis is rendered less vague, more definite. Even in cases of this order of simplicity, where, during ontogeny, we see a direct and all-powerful reaction of one single organ upon another, the physical means of interaction between the pair of correlated organs is not the same in every case. This must be kept in mind when we come to deal with the exceedingly difficult cases of phylogenetic moulding or adaptation.

SPEMANN'S CRITICISMS OF THE HOMOLOGY CONCEPTION

In a special article on the vexed subject of homology Spemann (1915) has utilized some of these experimental results to criticise not only the conception of homology in itself but also, apparently, Lankester's distinction between homogeny and homoplasy.

Citing his own experiments and those of Lewis on development of the lens, he points out that the lenses in the experimental cases are not homologous with normal lenses; nor are they homogenetic; they are, however, homoplastic. But, he says, the experiments also lead inevitably to the conclusion that lenses formed in normal development are both homogenetic and homoplastic, whereupon he feels constrained to ask whether Lankester's distinction has any deeper meaning.

This obscure remark seems to mean one or other of two things. Either Spemann has failed to understand Lankester, or, reflecting on the bearing of his own experiments, he has been momentarily waylaid into a pessimistic, *cui bono?* frame of mind. We can hardly believe the latter, i.e., we can scarcely suppose that he doubts the fact of homogeny (he does not doubt homoplasy). The valid examples of homogeny are the group features common to two or more great assemblages of animals by which is determined their subordination under a common category. It is the steady and extraordinary persistence of structural similarity under all apparent disguises, under all variety of environment and adaptation, that created the science of morphology to begin with, and that later provided the chief argument for common descent and furnished the means for a natural classification of animals. Homogeny with its very specific implications is not a thing of moonshine. We are left to suppose that Spemann has simply misread his authority. Now, Lankester has well foreseen that homoplasy may in some cases coincide with homogeny, as

the following sentence shows: "Further, if, instead of similar parts in the same organism, we suppose the same forces to act on parts in two organisms, which parts are exactly or nearly alike and sometimes homogenetic, the resulting correspondences called forth in the several parts in the two organisms will be nearly or exactly alike." Not the least striking feature of Lankester's homoplasy is that, enunciated in 1870, it should now have been so aptly confirmed by experimental work.

Going farther than Haeckel, who gave expression to a similar difficulty, Spemann says, "In point of fact, when one probes more closely, it is perhaps in the rarest cases possible to decide with certainty whether homology or analogy is involved." Here of course he refers, not to the structural similarities between functionally equivalent organs of widely different forms (the classical cases of analogy), but to the multitude of finer structural correspondences between the parts of more closely related forms. While his statement is a qualified one, it is of interest as representing the new outlook that comes of experimental handling of the problems of bodily structure. A mere assertion of homogeny no longer suffices to account for a structural correspondence. Homoplasy, all unsuspected, may have been simultaneously at work.

When Spemann finally concludes that "the homology conception as understood during the historic period goes to pieces in our hands when we try to work with it in the causal sphere," he means simply to say that, notwithstanding all its past achievements, as an engine of further investigation it requires now to be supplemented by something more definite and determinate, something we can grip without the feeling that the instrument we hold is an insecure or wobbly one. No one will doubt that for preliminary, provisional determination of the major relationships of animals one to another, the conception of homology has been of incalculable service. It is when we come to examine into the *mechanism* underlying similarity or divergence, as the case may be, that the need of some further means of assistance becomes felt.

HOMOLOGY AND FUNCTION B

As we began the subdivision of this article by discussing physiological considerations, so it is proper that we should return to physiology before its conclusion. It will have become apparent that homology and similarity as regards Function *B* as a rule coincide. The question now arises: Do they always coincide? As test cases let us consider some examples.

The thyroid. Throughout the Vertebrata proper (Pisces, Amphibia, Reptilia, Aves, Mammalia) this ductless gland has the same essential structure, consisting of closed vesicles, in which a single layer of epithelium as a rule surrounds colloid material. Throughout the group it preserves the same topographical position and has the same embryological history, viz. it arises as a median ventral downgrowth from the pharyngeal entoderm between the first and second branchial pouches, i.e., about the level of the first aortic arch. Its functional attributes are equally uniform and distinctive. It shows a great avidity for iodine introduced into the circulation; it elaborates a highly specific substance, thyroxin, which contains iodine in organic combination and whose chemical constitution has not been completely elucidated. In its peculiar avidity for iodine and in the manufacture of thyroxin, its Function *B* may (in a measure) be said to be determined, for, apart from scattered portions of similar and similarly derived tissue in the region

of the neck, we know of no other gland that exhibits the same biochemical characteristics. Within the limits of distribution aforesaid we may therefore say that the thyroid gland displays a striking accordance of homology and Function *B*.

Comparative anatomy has however pushed the "homology" of the thyroid beyond the limits of the Pisces into the lower Craniata, or cyclostomes, into the Acrania (*Amphioxus*) and into the Urochorda or tunicates. Adult cyclostomes have a true thyroid; in the larval cyclostome, *Ammocoetes*, the thyroid is represented by a complicated glandular structure of unknown function, the endostyle organ, which opens into the pharynx by a wide duct, and from which at metamorphosis the thyroid follicles of the adult are derived. In close details of structure as well as in its topography the endostyle organ of *Ammocoetes* corresponds with organs of similar name in *Amphioxus* and in tunicates (cf. D. Marine). The greater elaboration of structure of the endostyle organ, coupled with its free communication to the pharynx, undoubtedly indicates a difference in its intrinsic mechanism as compared with that of the thyroid.

Dismissing from our minds the unusual interest and suggestiveness of this particular morphological finding, let us confine ourselves to the purely formal question with which we started. It is plain that while the endostyle organ of these three types may be said to be homologous one with another (and then chiefly in the sense of positional homology), one cannot assert that the endostyle organ itself is, in any received sense of the word, homologous with the thyroid. We should rather phrase the matter by saying that the thyroid of the adult lamprey finds its Anlage in some part of the endostyle organ of *Ammocoetes*, or simply that the thyroid is a derivative of the endostyle organ. Just at the point, therefore, where the word homology proves inappropriate to express the nature of the relation, a difference in respect of Function *B* makes its appearance.

The medullary tissue of the adrenals. The adrenal glands of mammals, consisting of two parts, cortex and medulla, have a complex mode of development. The cortex, homologous with the interrenal body of elasmobranchs, arises from mesoderm cells of the genital ridge. The medulla, represented in fishes by the segmentally arranged "paired bodies," is derived from cells which belong to the same neuroblast masses as give rise to the nerve cells of the sympathetic ganglia. Throughout the group of the Vertebrata this medullary tissue presents the appearance of an endocrine organ. It strikes a brownish yellow color on treatment with salts of chromic acid (chromaffin reaction) and on extraction yields a hormone, adrenaline, whose chemical constitution has been fully determined. The hormone, from whatsoever vertebrate derived, exercises in mammals very specific pharmacological effects, which are the same as those produced by electrical stimulation of the nerves of the thoracico-lumbar sympathetic outflow. Here, therefore, we have a case of morphological or embryological homology with (so far as tests have hitherto gone) complete similarity of intrinsic physiological mechanism throughout the vertebrate group.

Islet tissue of pancreas. Among the secreting alveoli of the pancreas of vertebrates, and derived from the same endodermal Anlage as the pancreas, are multitudinous patches of a peculiar variety of tissue, the so-called islets of Langerhans. The cells of this tissue, which show affinities for particular stains and are of two recognisable types, have no

acinar formation, their disposition and vascular arrangements suggesting an endocrine function. In teleost fishes the islet tissue is particularly distinct, being encapsuled and occasionally present in masses of considerable size, which permit of ready isolation from the rest of the pancreas; in other vertebrates the islet tissue is intermingled with the alveolar. In its topographical arrangement, in its structural characters, and in its embryology, this islet tissue is similar or homologous throughout the group.

The functional attributes of this tissue are also distinctive and specific. No matter from what vertebrate it is obtained, an extract of the material lowers the percentage of sugar in the blood, promotes storage of glycogen in the liver of a diabetic and allows of utilization of glucose by the tissues, in virtue of which actions it can temporarily restore to normal the defective carbohydrate metabolism in cases of diabetes mellitus. At one time it was claimed that the islet tissue is merely a functional phase of the alveolar epithelium of the pancreas, that it can be transformed into alveolar epithelium and vice versa; all the available evidence goes however to show that while the two varieties of tissue owe their ultimate origin to one and the same mesoblastic Anlage, an early differentiation occurs, the one form becoming quite distinct from the other, with no possibility of reciprocal transformation (see Bensley). The two varieties of tissue are structurally and developmentally distinct and independent, and their functional attributes are similarly distinct and independent.

The foregoing examples of endocrine organs have been cited, partly because of the precision with which we can characterise their respective activities, partly because of the abundance, unusual in a physiological question, of comparative experimental data. Other endocrine examples, less definite in detail but all pointing in the same direction, might have been adduced. It will be noted that the criterion of similarity in respect of Function *B* on which we have relied is identity of a highly specific chemical or pharmacological product. The criterion itself is not beyond cavil; from industrial chemistry one might furnish endless illustrations of identity of product based on entirely different manufacturing processes, i.e., on entirely different intrinsic mechanisms; furthermore, we know that closely similar biochemical products, e.g. diastatic and proteolytic ferments, may be elaborated by very different types of organism, vegetable and animal, and therefore quite conceivably by different intrinsic mechanisms. In a difficult and involved scientific question it is sometimes possible however to err in the direction of undue caution. Most people would probably be willing to concede that in the cases cited the test of identity as regards Function *B* is appropriate and adequate.

The poison-glands of snakes might also be cited as organs whose mechanism is in a way particularised by the peculiar pharmacological products they yield. The active constituents of a venom are bodies allied to proteins, any given venom being a complex mixture of different albuminous toxins, which, roughly separable by physical or chemical means, are distinguished one from another as yet only by biological test. Two main categories of snake-poison, colubrine and viperine, are recognized by their action, but the pharmacological distinction between them is not hard and fast like the naturalists' distinction between the group of viperine and the group of poisonous colubrine snakes from which they are in each case derived. Apart from other poisons of animal origin, it may be said

that no pharmacological substances exhibit exactly the same array of biological reactions as snake-venoms; in other words, they are specific or distinctive products. It has often been stated that the poison-glands of snakes are homologous with the parotid glands of mammals, and this particular example was long considered by the author as a crucial case, rendering untenable the supposition that homology and intrinsic functional mechanism always coincide. Owing to their different innervation the venom-glands of snakes are now known not to correspond to the parotid gland of mammals. As to their origin, Wiedersheim says that they "become differentiated from" the upper of the two pairs of labial mouth glands common to reptiles. We thus see that in accordance with the individuality of their intrinsic functional mechanism they have no known homologues in other animals.

The cerebral cortex. As another case let us take the grey matter on the surface of the mammalian cerebrum, the so-called cerebral cortex. This is spread over the surface in a layer whose thickness and general cellular composition present an appearance of unusual uniformity. At the same time experiment has displayed a definite association of particular functions with particular areas of the cortex, one region controlling voluntary movements of different parts of the body, another being concerned with conscious vision, another with hearing, and so on. It is plain that the intrinsic mechanism of these different regions must vary. An area whose duty is to control voluntary movement must differ in ultimate action from one which receives and interprets visual impressions. One of the achievements of recent histological examination, beginning with Cajal and continued by A. W. Campbell and by Brodmann, has been to show that on a basis of simple histological structure the cortex may be mapped into a large number of regions, each with its own distinctive characters. Instead of being of uniform texture it is a mosaic of areas of different histological pattern. While this field of tedious and time-consuming histological work is as yet in its infancy and hard and fast statements can scarcely be made, in two cases at least, viz. that of the motor region and of the visual region, the limits as histologically defined correspond with those experimentally determined.

The facts with regard to the motor area are of especial interest in this connection. At quite an early period of investigation of cerebral localization Bevan Lewis and Henry Clarke, on the basis of a histological difference between the pre-Rolandic and the post-Rolandic cortex, concluded that the motor region proper lies in front of the fissure of Rolando. This deduction did not agree with the findings of subsequent experimenters, who, using strong electrical stimulation obtained motor effects on excitation of the cortex both behind and in front of the Rolandic fissure. The histological communication of these authors was in consequence ignored. Grünbaum and Sherrington, employing a more refined experimental technique, eventually proved that the motor area is strictly limited to the pre-Rolandic region. In this case histological differentiation between two areas had been able to indicate differences in their function which took more than twenty years fully to confirm. J. S. Bolton by histological methods first determined the exact limits of the visuo-sensory area of the cortex, which limits corresponded with those already established by the method of combined stimulation and ablation.

We should have no hesitation in naming

the motor, the visual or the auditory region respectively of the brain of man and of anthropoid apes as homologous each to each. They have homology of position, homology of development, and, as the investigations of A. W. Campbell show, they have in each case essential identity of intimate structure. As we cannot doubt that their intrinsic cellular mechanism is in each case of similar character, this example also goes to show that homology and Function *B* invariably coincide.

An additional criterion of homology. The truth is, wherever we inquire, the vaguely defined thing that we call homology implies identity of intrinsic mechanism in the homologous parts. We thus obtain a new—and, be it noted, a very sharp—criterion of homology, based not on position nor on embryological evidence, but on physiological similarity, and the test of such similarity is an experimental one. When Geoffroy in his notable attempt to clarify the problem of morphology discarded analogy, he was guided by a true instinct. Not so, when in his ignorance of the potentialities of physiology he waved all physiological considerations aside. His connection with the problem is merely a fine example of the thesis, elaborated by Sir J. G. Fraser in his "Psyche," that methods and institutions in themselves open to patent objection may at an early phase of culture exercise a very wholesome and salutary effect.

The new criterion applied to classification. It were tempting at this juncture to stop and point out that in the classification of animals considerations pertaining to Function *B* can furnish significant and suggestive data. Without even specifying any of the usually cited facts of formal structure one might define the group of Vertebrata, for example, in terms of common erythrocytic, common splenic, common thyroid, common pancreatic-insular, common adrenal, common hypophyseal and common labyrinthine function; the Tetrapoda in terms of superadded parathyroid and, possibly, bone marrow function; the combined group of Sauropsida and Mammalia in terms of the common maintenance and attachment function of their stratum corneum; the Sauropsida in terms of common purin metabolism; the combined group of Aves and Mammalia in terms of common homoiothermism; the Mammalia in terms of common lacteal function; the Eutheria in terms of common luteal function. Similarly with other animal phyla and their subdivisions. The systematic text-books of the future will no doubt develop and extend these physiological criteria of resemblance and of difference. When, too, it has once become possible to interpret the physiological significance of the various combinations of structural characters that now define the different animal groups, our present systems of classification will take on a new meaning. For the present, however, it is more important to proceed a stage further in our inquiry with regard to the specific problem at issue.

ONTOGENETIC AND PHYLOGENETIC FLUX

It has been pointed out how the new science of embryology introduced into the problems of morphology the idea of flux. No sooner had embryology become well established than Darwin imported into the subject still another fluxional conception. The various animal species, having evolved from ancestral forms dissimilar to them, are not themselves fixed or static entities. Rather, they represent temporary phases in a continuous line of progressive change. Morphology has thus to take cognisance of ontogenetic flux and of phylogenetic flux.

The homology conception arose when animal forms were believed to be fixed or static. The introduction of embryology failed in any way to modify the conception of homology. The embryological criterion of homology was not due to embryology as such.

With the advent of Darwinism a forward step was made. In its implications for morphology ontogenetic flux was now for the first time taken into practical account. An attempt, confused but still definite, was made to incorporate "embryological homology" as a method into the working equipment of the subject. The recognition of phylogenetic flux led at first to no new practical method of its own, just as the introduction of embryology on a previous occasion led to no new morphological method.

Lankester's effort was both critical and constructive. His homogeny is static, much as the primitive positional homology was static. The recognition of plasis, limited as was the use he made of the idea, is his important contribution to the conception of organic flux, and in the very general terms of its formulation his homoplasy is applicable both to ontogenetic and to phylogenetic flux. Later came *Entwicklungsmechanik* with its strictly ontological experiments, which on ontological territory have confirmed and rendered much more definite Lankester's hypothesis.

With it all, we still lack a means of treating phylogenetic flux, which, be it noted, is the great outstanding problem of formal morphology. In this type of flux we recognize the occurrence of two quite different things. One is modification of existing structures by way of adaptation to new uses; throughout these modifications the intrinsic mechanism remains essentially the same and the parts remain homologous. The other is the invention or evolution of structures of a quite new type, whose intrinsic mechanism is also new. It is true, the new structures, which show novel biophysical or biochemical behavior, themselves grow out of the old. While the process by which they are produced is entirely obscure, their apparition denotes a different kind of event from any simple successful application of an existing structure or system of existing structures to a new purpose.

Distinct as the foregoing two problems are—that, namely, of modification by simple adaptation and that of brand new invention—both are problems of plasis in a wide sense. It should always be kept in mind that homoplasis or analogy is only one limited aspect of a more comprehensive plasis. Analogy, notwithstanding its great and unexploited potentialities for the study of plasis, is, so to speak, an accidental affair. Only in certain cases will the modifications achieved in two different forms closely resemble each other.

Exclusive preoccupation with the homology method has been responsible for a certain narrowness of vision among those who handle animal structure. There has been a tendency to consider animals merely as ringing the changes on a fixed or preordained equipment of structure. Bateson was the first to push this philosophy to its logical conclusion and to assert, with what degree of conviction no one can quite make out, that evolution proceeds by dropping of characters rather than by acquisition of new characters. Of course, this whole philosophy is wrong. The inventiveness of animals is not exhausted in the extraordinary way in which they can bend or mould existing equipment to new uses. They can equally well, departing from precedent, hammer out inventions of a

kind that is entirely new, and this they have done over and over again.

While no one would dispute that the science of morphology has been erected on the conception of homology, it is also clear that the help obtainable from homology in any study of animal structure is of a restricted kind. Homology is at best an inference originally forced upon comparative anatomy by its material. It is an inference that arises mainly from similarities; from dissimilarities only in so far as these serve as a background or contrast to the similarities. Practically speaking, it is an effective method of classification. It serves to disentangle any large assemblage of forms and to group structurally similar forms under common categories. Rationally speaking, it does not in any way explain the similarities which gave it birth. Even for purposes of classification it has been of assistance only in laying down the broad features of similarity of the larger groups. It has been of little real service in assessing the nature of the gaps between widely divergent types. For finer familial, generic and specific distinctions it is scarcely ever used, because it does not profess to deal with dissimilarities. At the same time our whole knowledge of evolution, which is fundamental for any science of animal structure, teaches us that a critical phase of the evolutionary process lies in the origin of varieties and of new species.

Because homology, and for that part analogy, deal only with similarities, they are both defective principles in the face of developing diversity. As divergences arise not discontinuously but by slow gradation (we are now speaking in phylogenetic terms and are not raising the issue of mutations, which from our present point of view is a secondary matter), it is clear that simple static homology and analogy do not provide any infinitesimal calculus that can be applied to the question of flux, i.e. to the birth and continuous development of dissimilarity. If the systematic study of structure is to go on advancing, homology must be reinforced, analogy, in its limited field of operation but from the plastic point of view, must receive its full meed of consideration, while attention must be directed to differences as much as to similarities.

Experimental embryology has already applied itself to the problem of ontogenetic flux. Except by implication it has not touched upon phylogenetic flux. We are aware that phylogenetic flux in some way dominates and sets the character of ontogenetic flux. So far as one can say, it is primary, ontogenetic flux being secondary. For the intimate study of phylogenetic flux the one ready instrument to our hand is physiology. An example or two may suffice to illustrate the matter.

The sulcus lunatus of the Chinese brain. By gross examination of the sulci and of the sectioned cortex, Shellshear has recently shown that the occipital region of the Chinese differs as a rule from that of the European brain. In the Chinese brain a clearly marked sulcus lunatus or "Affenspalte" extends well out on to the lateral surface of the occipital lobe. In most cases its posterior lip forms an operculum, and the stria of Gennari, which characterises the "visuo-sensory" region of Bolton, extends to the posterior lip of the sulcus. Thus in the Chinese brain the stria of Gennari, instead of being limited to the mesial aspect of the occipital lobe as in Europeans, spreads on to the lateral aspect. It is a common saying among the Chinese themselves that their vision differs from that of Europeans. In looking directly forward they claim to have a clearer perception of what is

happening in the peripheral field of vision than do Europeans. Their art objects too are more crowded with detail than are the corresponding productions of the white races of mankind. It is true that Shellshear in his purely anatomical exposition refrains for the moment from making any functional comparison, but if some difference of the kind indicated should also be found by appropriate physiological experiment to exist between Chinese and Europeans, it is plain that we should here have a means of observing and tracing structural and functional flux within the limits of one and the same species. The numberless recorded observations of anatomical differences between the different races of mankind have also no doubt their functional counterpart, though methods of experimental comparative treatment are as a rule less immediately obvious than in the particular case just cited.

The odor-secreting glands of mammals. In his article, "Mammalia," in the ninth edition of the *Encyclopaedia Britannica* Flower has collected together a list of odor-secreting glands connected with the skin of various mammals. His statement is as follows: "To this group of structures belong the suborbital gland or 'crumen' of Antelopes and Deer, the frontal gland of the Muntjak and of Bats of the genus *Hipposiderus*, the submental gland of the Chevrotains and of *Taphozous* and some other Bats, the post-auditory follicle of the Chamois, the temporal gland of the Elephant, the lateral glands of the Musk-Shrew, the dorsal gland of the Peccary, the inguinal glands of Antelopes, the preputial glands of the Musk-Deer and Beaver (already alluded to in connection with the use made of their powerfully odorous secretion in medicine and perfumery) and also of the Swine and Hare, the anal glands of Carnivora, the perineal gland of the Civet (also of commercial value), the caudal glands of the Fox and Goat, the gland on the humeral membrane of Bats of the genus *Saccopteryx*, the post-digital gland of the Rhinoceros, the interdigital glands of the Sheep and many Ruminants, and numerous others. In some of these cases the glands are peculiar to, or more largely developed in, the male; in others they are found equally developed in both sexes." In this striking series any question of homology between the different glands is excluded because of topographical reasons. Yet the glands in question form a related group, being derivatives presumably of sebaceous glands and subserving somewhat similar uses. At the same time each is obviously an independent invention, and the odors or chemical products elaborated differ one from another. How should one set to work to extract from such a series further information respecting phylogenetic flux? Clearly one must first invoke physiology and biochemistry.

The great trouble with morphology as a guide in the elucidation of animal form, or even as a means of approach to structural and evolutionary problems, is that it is silent as to the mode of operation of the structures with which it professes to deal. Imagine a refined morphology of the brain of mammals, based purely on comparative criteria gross and microscopic, but which fails to envisage the experimental results of the workers on cerebral localisation, ranging from Fritsch and Hitzig to Henry Head, or of the workers on cerebral "educability," from Goltz to Pavlov! The one thing that gives life and meaning to the comparative anatomical knowledge of the cerebrum and saves it from being an arid collection of maps and diagrams, is the physiological work that has proceeded *pari passu* with the anatomical. Indeed the time and ef-

fort spent on the details of neurological anatomy is justified only when the work is meant to be brought into correlation with the physiological. What holds true of a pure morphology of the brain holds equally true of morphology generally. Morphology finds a meaning only in its functional setting. At our present stage of history it is easy for us to see that the original decision to separate physiology from comparative anatomy was foredoomed to failure.

PLASIS

In view of the preceding exposition it is plain that the broad process here called plasis, the process to whose investigation the experimental embryologists have already devoted themselves in the field of ontogeny, is equally insistent in the realm of phylogeny. We have seen how Lankester, a Darwinian and believer in natural selection, was early constrained to postulate special environmental "forces" in order to account for certain aspects of phylogenetic plasis. There can be little doubt that plasis is a controlled process and proceeds according to law. Granted the fact of evolution, the astounding fit between the animal as a whole and its environment, and the correspondingly wonderful internal adjustment of all its diverse parts one with another, seem to indicate the operation of (physical) law. Endlessly complex as animal structure is, the dominant principles involved in maintaining the structure or in changing it according to need, may be few and relatively simple.

Roughly speaking and without attempting at the moment any further sifting of detail, we may recognize three (or four) elements in phylogenetic plasis: (1) the power to transmit by heredity the temporarily existing condition of structure; (2) adaptive modification of existing structure; (3) the invention of new structures; to which we may add, whether an independent thing or not, (4) the occasional dropping of existing characters. Thanks to the work of the school of T. H. Morgan and to the investigations of Goldschmidt, our knowledge of the mechanism of (1) is rapidly becoming more precise and definite. We may also have some possible knowledge of the mechanism of (4), but scarcely yet of (4) in its adaptive implications. The conditions that control (2) and (3) remain quite obscure, and these are the very elements that have not yet been subjected to the rigorous physiological mode of inquiry. Lucas has sought to sketch a method whereby one might begin with the investigation of (3). In the course of our present exposition we have obtained a physiological test for homology, which implies that we have a better means than before of observing the operation of (2).

The failure up to the present to establish by experiment the transmission of "acquired" characters may well be due to the paucity of our knowledge respecting (2) and (3). It has often been suggested that our laboratory attempts to cause phylogenetic modification may not have taken account of an adequate time factor. Apart from the question of time there is another possible way of looking at the matter. Any given animal is a system in equilibrium with its environment, and is built up of a vast congeries of systems all in equilibrium with each other. To use a very rough illustration, the organism might conceivably be likened to a complex jointed linkage, which is poised or balanced at some central region, all its various outlying parts being similarly poised but so interconnected that an adequate disturbance of one or more may cause a rearrangement of the whole with

consequent new position of total equilibrium. In each kind of animal this complex equilibrium is different; in any two closely related species the equilibrium has taken a different cast or set; and the differences increase as we pass in succession from the species to the genus, from the genus to the family, and so on. We know, too, that these equilibrium differences are even tied up with chemical differences in the body proteins of the various organisms. Now, experience has amply taught us that the structural parts of any animal may be crudely mutilated without damage to the essential, specific or phylogenetic, equilibrium. So, too, did the atoms of terrestrial chemistry remain in equilibrium, notwithstanding all kinds of apparent rough usage, until Rutherford discovered a means of bombarding them in a special way. We may not yet have hit upon the proper type of bombardment effectively to upset the specific or phylogenetic equilibrium. We may not be clear as to what constitutes an acquired character in the sense of phylogenetic modification, and in our experimental attempts at phylogenetic modification we may have been dealing only with *trivial characters, not with any of the* pivotal equilibrium-deciding factors.

Mere speculation is however a profitless matter. Enough has perhaps been said to enable a physiological reader to realize that his subject is intimately involved and can render important assistance in some of the wider issues concerning comparative anatomy and the process of evolution. The great service rendered by comparative anatomy, apart from furnishing material in proof of evolution, has been to raise problems which it does not of itself possess the means of solving. Without recourse to experiment the ultimate issues must necessarily remain unsettled. The eventual solution of the broad problem of adaptation, or what we have here called plasis, would seem to lie with the physiologist, provided only that he were willing to give his deliberate attention to comparative problems. It might equally be with the comparative anatomist, provided he should adopt the discipline and the methods of physiology.

LIST OF LITERATURE

Bateson, W. 1914. Report of the Eighty-fourth Meeting of the Brit. Assoc. for the Advancement of Science, (3–38).

Bensley, R. R. 1914–1915. Harvey Lectures, Series X, (250–289).

Bolton, J. S. 1900. Phil. Trans. Roy. Soc., Sec. B., 193, (165–222).

———. 1909. Further Advances in Physiology. London, E. Arnold, (284–350).

Braus, H. 1904. Verhandl. d. Anat. Gesel., Anat. Anz., Erg—Bd., xxv, (53–65).

———. 1905. Anat. Anz., xxvi, (433–479).

Brodmann, K. 1903–1907. Journ. f. Psychol. u. Neurol., Bd. 2, 4, 6, 10, various communications.

Campbell, A. W. 1905. Histological Studies on the Localisation of Cerebral Function. Cambridge University Press, 360 pp.

Carlson, A. J. 1904. Amer. Journ. Physiol., xii, (67–74).

Gaupp, E. 1913. Kultur der Gegenwart. Zellen- u. Gewebelehre, Morphol. u. Entwicklungsgesch., II. Zoologischer Teil, (446–447).

Grünbaum, A. S. F. and C. S. Sherrington. 1901. Proc. Roy. Soc., lxix, (206–208).

———. 1904. Ibid. lxxii, (152–155).

Lankester, E. Ray. 1870. Ann. Mag. Nat. Hist., (4), vi, (35–43).

Lewis, W. H. 1904. Amer. Journ. Anat., iii, (505–536).

Lewis, Bevan and H. Clarke. 1878. Proc. Roy. Soc., xxvii, (38–49).

Lipschütz, A. 1919. Die Pubertätsdrüse und ihre Wirkungen. Bern.

———. 1924. Compt. rend. soc. biol., xc, (274–276).

———. 1925. Pflügers Arch., Bd. 207, (548–562).

Lucas, Keith. 1909. Science Progress, (1–12, 321–331).

Marine, D. 1913. Johns Hopkins Hospital Bull., xxiv, (135–141).

Osborn, H. F. 1907. Evolution of Mammalian Molar Teeth. Chap. X, pp. 228–239.

Russell, E. S. 1916. Form and Function. London, John Murray, 383 pp.

Shellshear, Joseph L. 1927. Journ. of Anat., lxi, (1–13).

Spemann, H. 1901. Verhandl. d. Anat. Gesel., Anat. Anz., Erg—Bd., xix, (61–79).

——. 1905. Zool. Anz., xxviii, (419–432).

——. 1907. Ibid., xxxi, (379–386).

Spemann, H. 1915. Kultur der Gegenwart. Allgemeine Biologie, (63–86).

Steinach, E. 1912. Pflügers Arch., cxliv, (71–108).

——. 1910. Zentralbl. f. Physiol., xxiv, (551–566).

——. 1913. Ibid., xxvii, (717–723).

Tait, John (a). 1917. Proc. Roy. Soc. Edin., xxxvii, (69–94).

—— (b). 1917. Proc. Roy. Soc. Edin., xxxvii, (246–303).

Tait, John and W. F. Emmons. 1925. Proc. Roy. Soc. Edin., xlv, (42–47).

Willey, A. 1911. Convergence in Evolution. London, John Murray.

THE HISTORY OF WHALES—THEIR ADAPTATION TO LIFE IN THE WATER (*Concluded*)

By REMINGTON KELLOGG

Bureau of Biological Survey, United States Department of Agriculture

PLATANISTIDAE

THERE does not appear to be any single directive trend in the line of development that regulated the overlapping or telescoping of the major bones in the odontocete skull, but on the contrary telescoping has given rise to many different types of skulls, and of these none are more unusual than that of the Maryland Miocene porpoise, *Zarhachis flagellator* (Kellogg, 1924; 1926). An extreme stage in the lengthening of the rostrum is represented by this skull, and appears to mark the culmination of the long-snouted type of porpoise. The skull is nearly four feet long with the rostrum fully five times as long as the braincase. Mechanical difficulties would interfere with a further lengthening of this type of rostrum. While the family position of this porpoise may be a matter of personal opinion, the periotic bone is similar to that of *Platanista*, and cranial peculiarities also indicate that it should be referred to the family Platanistidae.

According to our present knowledge, *Zarhachis flagellator* represents a highly specialized aberrant type that possesses certain fundamental characters in common with the living Ganges porpoise *Platanista gangetica*. No fossil porpoises of this type have been described from Miocene formations of Europe and it may have been a migrant from some other region, possibly the South Atlantic, which came into association with the more widely distributed types during the latter part of the Miocene period. In its general features the skull of *Zarhachis* is characterized by the presence of a pair of crescentic orifices inclosed by ectethmoids on the anterior wall of the braincase; maxillaries expanded laterally behind the antorbital notches with their lateral borders turned upward to sheath the internal surfaces of the up-built supraorbital processes of the frontals, and in contact posteriorly with the supraoccipital; small elevated vertex; pterygoid with well developed external reduplication, which extends from the squamosal to the median line of palate at a level considerably in advance of antorbital notch, concealing the alisphenoid and palatine bones; palatine bone forming part of the anterior wall of narial passage; total number of teeth in excess of 300; the enamel crowns of teeth ornamented with longitudinal striae and the roots slightly thickened. The symphysis is equivalent to more than two-thirds of the total length of either mandibular ramus. The cervical vertebrae are free, and the dorsal and lumbar vertebrae have broad flattened neural spines. The path or paths of development followed by the descendants of this extinct porpoise are unknown at the present writing.

The existing *Platanista gangetica*

undoubtedly traces its origin back to some extinct porpoise in which the outer borders of the maxillaries were turned upward above the orbits. This peculiar structural condition permitted the maxillaries to grow upward, resulting in the formation of the odd incurved fan-like anterior teeth have a high pointed crown and a broad laterally compressed root. The relations of the basicranial bones suggest that the rostrum and braincase have been telescoped to a greater extent and in a somewhat different manner than in other porpoises. To recapitulate the

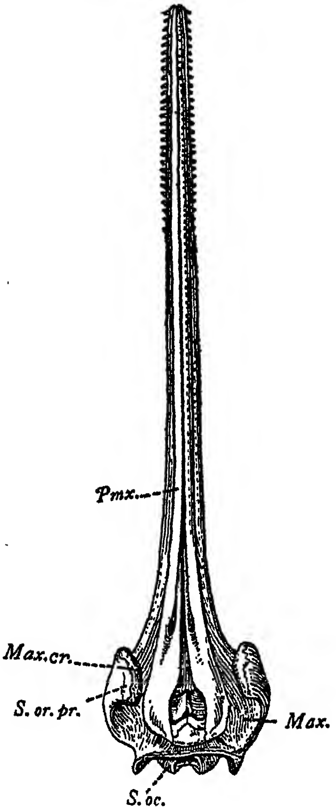


FIG. 12

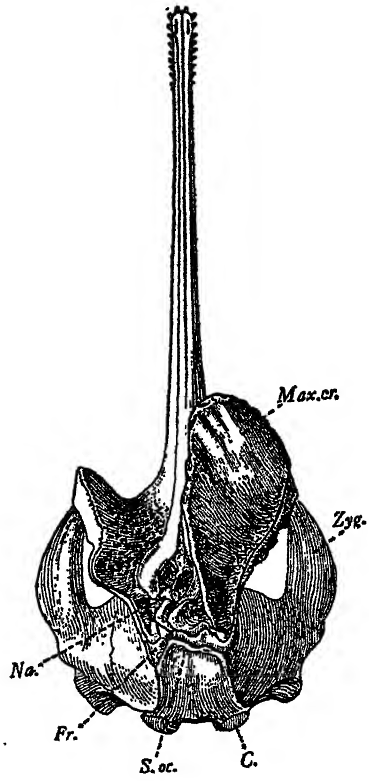


FIG. 13

FIG. 12. DORSAL VIEW OF SKULL
Zarhachis flagellator, Middle Miocene, Maryland
FIG. 13. DORSAL VIEW OF SKULL
Platanista gangetica, India. Left maxillary crest removed to expose upper surface of cranium

maxillary structures seen in the living *Susu*, which cover the facial depression like a mask. The rostrum is so slender and the palate so narrowed that the upper tooth rows lie side by side, and in old individuals apparently merge together at the posterior end of the series. The evidence supporting this observation it may be pointed out that in correlation with the depression of the rostrum below the level of the braincase, the narial passages have moved backward and are situated on a level with the anterior margins of the squamosals, the pterygoids

and their external reduplications extend forward to the level of the antorbital notches and thus entirely conceal the palatine and alisphenoid bones, the opening for the infraorbital canal is within the temporal fossa, the zygomatic process is placed far forward and its extremity is in contact with the supraorbital process of the frontal, the antero-posterior diameter of the latter has been shortened and the process as a whole deflected obliquely forward as would be expected to result from a lowering of the rostrum, and the lachrymal bone has been pushed inward and mortised into the maxillary instead of being inserted between the maxillary and the supraorbital process of the frontal.

PHYSETERIDAE

The most singular sort of odontocete development is found in the physeteroid porpoises, which begin their career, so far as known, in the Lower Miocene with skulls that possess all the structural details of their successors in later geological stages. It is confidently believed that these somewhat generalized sperm whales had been differentiated from the main odontocete stock subsequent to the elimination of the postorbital constriction, but at a time long before the beginning of the Miocene, and that many of the diverse types that flourished in later Miocene seas trace their ancestry back to as yet unknown types of extinct physeteroids. The living sperm whale (*Physeter catodon*) has an enormous reservoir on the top of the head, surrounded by a fibrous integument, and divided interiorly into compartments, which communicate with one another and with cells or sinuses also filled with liquid oil or spermaceti. Beneath this reservoir, which may contain 10 to 15 barrels of liquid oil, is a great mass of fibrous cellular tissue, likewise saturated with spermaceti, known as the adipose cushion. Spermaceti, however, is not always present, for occasionally cachalots are killed that are "dry." If any reliance may be placed on analogous structural conditions in the living sperm whale the structural details of these early physeteroid skulls had been adjusted to lodge a developing fat or spermaceti cushion. Even in the Lower Miocene *Diaphorocetus* the adipose cushion had grown around the right side of the narial passage, and as a result of this peculiar condition the relative proportions and relations of the bones forming the dorsal surface of the skull had been altered in a strange manner, producing a huge supracranial basin, which was bounded behind by the supraoccipital and laterally by the elevated borders of the maxillaries. Most peculiar of all these modifications is the posterior expansion of the up-curved right premaxillary bone which overspreads the anterior wall of the "dished-in" braincase. The vertex has been entirely eliminated, the frontal bones are depressed along the median line, one of the nasal bones has been either lost or greatly reduced and the other flattened against the frontal behind the greatly enlarged left narial passage, and the rostrum has expanded laterally at the base. The roof of the braincase seems to have been depressed below its original level because of the additional weight and pressure of the developing adipose cushion.

The oldest known Miocene physeteroids as well as some of the later ones have teeth implanted in distinct alveoli in the maxillary and premaxillary bones. The premaxillaries form the extremity of the rostrum, and three teeth are implanted in each bone. In the course of geological time we observe that there is a tendency among certain types for the teeth to become loosely implanted in rather large alveoli, and this condition is accompanied

by a corresponding decrease in the thickness of the intervening septa. These septa finally disappear, leaving an open alveolar gutter in the maxillary. The growth of the maxillary teeth is arrested, and a hypertrophy of the dentition ensues. Functional teeth are not present in the upper jaw of the living sperm whale, *Physeter catodon*, but as many as eight atrophied teeth are sometimes found buried in the gum. Conversely other extinct types of physeteroids retain a functional dentition in the upper jaws to the close of their relatively brief life span. The mandibular teeth of all known physeteroids are implanted in distinct alveoli. Whether or not a narrowing of the mandibular symphysis brought about an increased effectiveness of the teeth in the lower jaws no one knows, but it is nevertheless true that the great lateral broadening out of the maxillary carried the upper tooth rows outside of the normal occlusal position of the upper and lower cheek teeth. The teeth of these early Miocene physeteroids are much larger than those of contemporary odontocetes, and it would seem that they were employed as much for tearing as for seizing. Killer whales (*Orcinus*) tear away portions of the flesh of their victims by quick powerful jerks, and it is quite probable that the earlier sperm whales tore their food apart in a similar manner. It is evident that the earlier Miocene delphinoids were likewise predacious, but their slender teeth were adapted for seizing and holding slippery prey, such as fish.

Two skulls, representing different genera of physeteroids, are known from the Lower Miocene Patagonian formation exposed along the coast in Chubut Territory, Argentine Republic. The smaller of these, *Diaphorocetus poucheti* (Moreno, 1892) measured when complete about three feet in length. It possessed teeth in both jaws, for which there were more than 14 alveoli in each maxillary bone. The occiput of this skull is obliquely truncated, each maxillary bone is perforated by large foramina along the lateral crest, the postnarial portion of the right premaxillary is broad, forming the medial surface of the posterior wall of the supracranial basin, and the lateral margin of the maxillary is not excessively thickened above the supraorbital process.

The other skull, representing *Idiorophus patagonicus* (Lydekker, 1894; Kellogg, 1925), is nearly twice the size of that of *Diaphorocetus*. It is characterized by the number and position of the maxillary foramina, the long laterally compressed extremity of the rostrum with arched premaxillaries, and the presence of teeth in both jaws. There are 22 teeth in each upper jaw, of which 19 are implanted in the maxillary and 3 in the premaxillary. Each mandible is provided with 24 teeth. The teeth average a little more than 4 inches in length, and their conical crowns are covered with rugose enamel. The long, terete, and but little curved crowns are equivalent to a little more than one-fourth of the total length of the teeth.

The reduction of the maxillary dentition had commenced as early as the Middle Miocene, for we have indisputable evidence that such was the case in the Temblor *Aulophyseter morricei* (Kellogg, 1927) found near Bakersfield, California. The shallow closely approximated alveolar grooves of the Temblor skull, occurring as they do with other cranial details that undoubtedly indicate a more advanced stage in the basining of the facial region, have suggested the possibility that if teeth were present in the upper jaws they were lodged in the gum as in the living sperm whale. The skull measures about four feet in length, and the distal constriction of the rostrum is coextensive with the

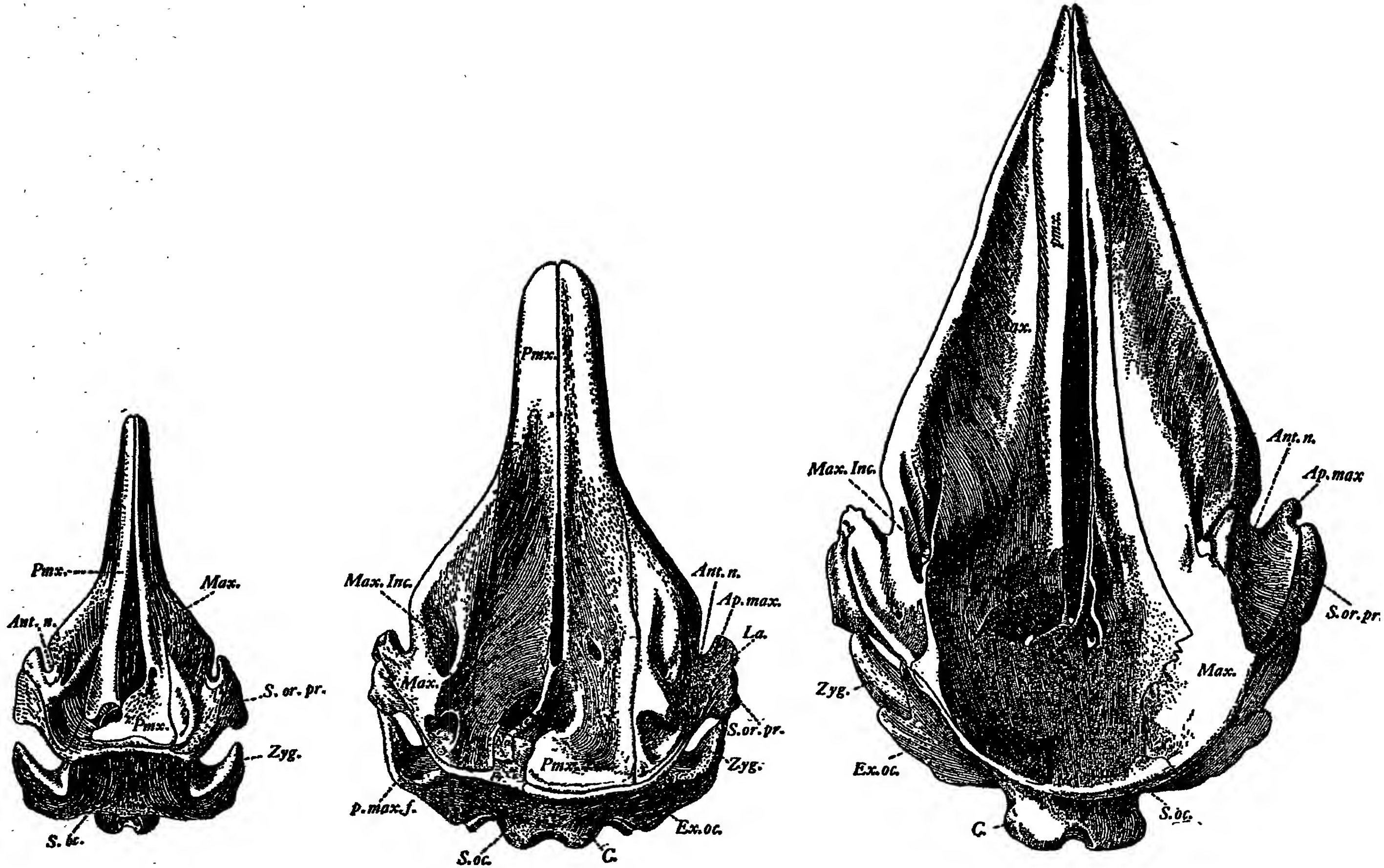


Fig. 14. Dorsal Views of Skulls

Diaphorocetus poucheti, Lower Miocene, Patagonia. *Aulophyseter morricei*, Middle Miocene, California. *Physeter catodon*, Tasmania, young male (after Flower).

shallow alveolar grooves. There is a large incisure and a smaller posterior foramen in each maxillary bone above the orbit.

Vastness of size is so generally associated in the popular idea with the whalebone whales that relatively few realize that gigantic species have been developed also among the toothed whales. Both giants and dwarfs may appear in whales constructed along similar lines. The living sperm whale, or cachalot, *Physeter catodon*, is the largest known odontocete, either living or extinct, and there is only one described Miocene species *Ontocetus oxymycterus* (Kellogg, 1925) that approaches it in the size of the skull. Comparative measurements indicate that a complete skull of this extinct physeteroid would measure more than 12 feet in length. The extremity of the rostrum was formed by the premaxillaries, and three large teeth were implanted in each. The largest mandibular teeth measure about 12 inches in length, and all of the teeth in both jaws were lodged in distinct alveoli. It should be noted, however, that the alveoli were too large and the roots too loosely fitted to hold the teeth in position independently of a dense ligamentous gum. The enamel on the crowns of these teeth is ornamented with coarse longitudinal striae.

Physeteroids with functional teeth in the upper jaws continued to near the end of the Miocene, when they seem to have disappeared from geological history. Their remains have been found in Upper Miocene deposits in Europe, North America, and Japan. The incomplete skull of *Orycterocetus mediatlanticus* (Cope, 1895; Kellogg, 1925) found in the St. Mary's formation at Drum Point, Maryland, has the lateral margin of the maxillary excessively thickened at the level of the orbit, but the positions of the maxillary foramina and the disposition of the maxillary alveoli are similar to the Lower Miocene *Idiorophus*.

The number of physeteroid types (Abel, 1905) found in the Upper Miocene black crag of the Antwerp basin, Belgium, is truly surprising in view of their scarcity in later geological formations. The distinguished Austrian palaeontologist, Professor O. Abel has recognized a rather large number of physeteroids in these deposits, including *Scaldicetus mortezelensis*, *Physeterula dubusii*, *Thalassocetus antwerpiensis*, *Placoziphius duboisii*, and *Prophyseter dolloi*. The skulls of these extinct Belgian physeteroids differ from one another in certain details of cranial construction, but all possess the large supracranial basin. The largest of these is *Physeterula dubusii*, whose skull measures less than six feet in length; each mandibular ramus is furnished with 20 teeth about 5 inches long, of which 12 are restricted to the symphysis. No enamel is present on the crowns of these teeth. The other species have somewhat smaller skulls, those of *Scaldicetus mortezelensis* and *Placoziphius duboisii* being less than 3 feet in length. In *Placoziphius* the upper teeth seem to have been completely lost, for the alveolar grooves are nearly closed. *Scaldicetus* on the other hand is said to have retained the maxillary and premaxillary teeth, and the unworn teeth of this physeteroid have the crowns covered with longitudinally striated enamel, in addition to vestigial crenelated cutting edges. The roots of these teeth are simple and have a rather large pulp cavity.

The culmination of the tendency toward the abnormal development of a spermaceti cushion may be observed in the living genus *Physeter*, the great size of whose skull is disproportionate, in respect both to the brain and to the body. In this genus, the spermaceti cushion has attained

an enormous size, and in correlation with this increase the bones comprising the rostrum have expanded horizontally. In life the disproportionately large head abruptly truncated in front, small eyes placed near the angle of the mouth, and blowhole on the edge of the muzzle, in conjunction with a dorsal hump give *Physeter catodon* a very unusual appearance. Skulls of adults measure 16 feet or more in length and have a continuous maxillary alveolar groove without any indication of septa. The large palatine bones do not form any part of the backward sloping narial passages, and are overridden posteriorly and mesially by the pterygoid bones. As many as 27 teeth are lodged in each mandible, and the symphysis is equivalent to half of either ramus. The posterior margin of the supracranial depression is more abruptly elevated in the physeteroids than in any other family of cetaceans, and the basin extends farther forward. In general the physeteroid skull may be defined as having the rostrum longer than the cranium, no sagittal crest, rise of anterior border of lateral wall of supracranial basin within the antorbital notch, small lachrymals, elongated jugals with styliform processes, expanded palatines, small pterygoids, and large foramina, which connect with the infraorbital system.

KOGIIDAE

It is not improbable that, when more is known of the immediate predecessors of the living odontocetes, the diminutive living *Kogia breviceps* will be found an offshoot of some early Tertiary physeteroid. At present we have no knowledge of their previous geological history. Compared with a sixty-foot cachalot, an eleven-foot pigmy sperm whale seems rather small. It has an attenuated snout, eyes placed nearer to the forehead, blowholes on the forehead, and a falcate dorsal fin. The skull of this porpoise is characterized by a short rostrum, a well defined sagittal crest, rise of anterior border of lateral crest of supracranial basin outside of antorbital notches, large thickened lachrymal fused with styliform jugal, small palatines, expanded pterygoids, and small foramina connected with the infraorbital system. The mandible has a short symphysis and is furnished with 14 or 15 teeth.

POSSIBLE ANCESTORS OF THE MYSTICETI

The least modified cetacean skull thus far collected is represented by *Archaeodelphis patrius* (Allen, 1921), whose critical peculiarities of detail agree more closely with mysticete than with odontocete cranial construction. Annectant types are lacking to connect *Archaeodelphis* with any known cetothere, and the details hereinafter mentioned should not be interpreted as implying that this Eocene cetacean was the source to which cetotheres of later geological stages owed their origin. The most that can be said is that *Archaeodelphis* and the cetotheres are derivatives of the same common stock.

Structurally this skull is much less modified than any known fossil or living whalebone whale. Obvious peculiarities of the *Archaeodelphis* skull are the large orbit, elongate flattened nasals and extremities of premaxillaries situated almost entirely anterior to the supraorbital processes of the frontals, long and forward sloping narial passages with distinct dorsal nasal cavities, broad intertemporal region, a triangular lachrymal extending laterally as far as or beyond the maxillary and overspread by the latter, and a maxillary with infraorbital and ascending processes. The position of the maxillary with respect to the lachrymal, the orbit, and the supraorbital process of the frontal

may be regarded as an early stage in the development of conditions like those now seen in the mysticetes. The maxillary has an infraorbital process that projects backward to the level of the optic canal, and the ascending process has not been pushed backward very far over the upper surface of the supraorbital process of the frontal. In its essential features this bone is typically the interlocking sort of maxillary found in all known whalebone whale skulls. A subsequent constriction of the ascending process of the maxillary would lead to the presence of pterygoid fossae for accessory air sinuses of the inner ear and a backward infraorbital extension of the maxillary are prerequisites for any precursor of the mysticetes. The presence or absence of teeth on the rostrum, which is unknown, while interesting is of relatively little importance, for embryology shows us that the predecessors of the mysticetes were toothed whales. In another important detail, this skull resembles those of whalebone whales, for it has a periotic bone with a long apophysis wedged in between the exoccipital and the squamosal.

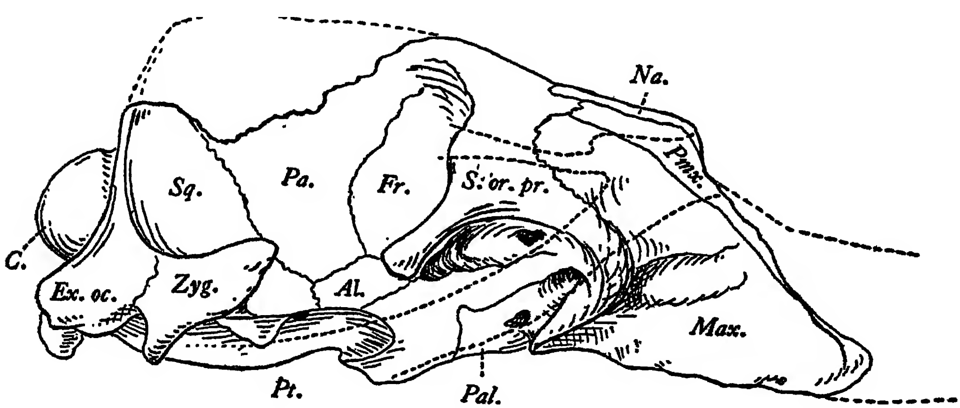


Fig. 15. Lateral View of Archaeodelphis patrius, Upper Eocene
Dotted lines indicate course of narial passages, narial cavity, and olfactory foramina

mysticete type of construction. The base of the ethmoid and the dorsal nasal cavities are roofed over by the nasal bones, and the palatine bones do not enter into the composition of the anterior walls of the narial passages, thus agreeing with the type of structure present in the mysticetes. The upper portion of the supraoccipital shield is destroyed, but it is evident that it has not extended forward far enough to meet the frontal. The parietals therefore form the vertex of the braincase. This skull has rather large pterygoid fossae, which agree in shape and position with those of mysticetes. The

At least one survivor, *Patriocetus*, of the archaic toothed whales has been found in the Aquitanian white sands of the Linz basin in Austria, along with *Cetotheriopsis*, the oldest known member of a family of primitive whalebone whales, the *Cetotheriidae*, and *Agriocetus*, whose exact relationships are still imperfectly known. The imperfect type skull and another fairly well preserved skull form the basis for *Patriocetus grateloupii*, which was thought by Professor Abel (1913) to be a precursor of the Mysticeti, but both are so coated with grains of sand that the sutures are obscured.

Whether *Patriocetus* belongs with the archaic toothed whales or whether it represents a precursor of the mysticetes are questions that have occasioned some difference of opinion. The deductions of Professor Abel and others on the mysticete relationships of *Patriocetus* are of little or no consequence in so far as the actual shape of the braincase is similar to *Archaeodelphis* and *Agorophius*. The most obvious peculiarity of the braincase of *Patriocetus* is the thin ledge-like projection from the parietal that extends backward from the supraorbital process to the supraoccipital and overhangs the temporal fossa.

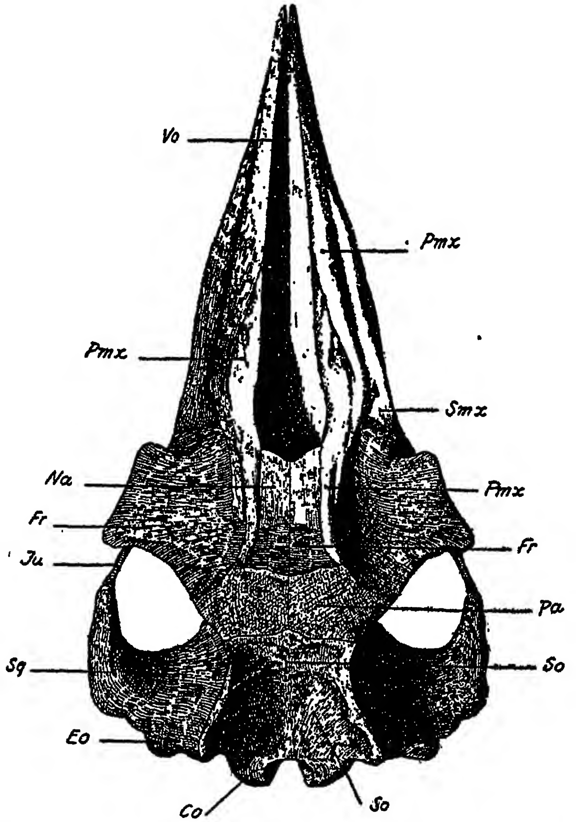


Fig. 16. Dorsal View of Skull of Patriocetus grateloupii, Upper Oligocene, Linz, Austria (After Abel)

precursor of the whalebone whales is concerned, for this cetacean was contemporaneous with at least one member of that group. The question to be settled, if possible, is whether or not the mysticetes passed through a stage of cranial architecture comparable to the restorations given by Abel. The published photographs indicate that the general

Several details of the restorations and description given by Abel are so contrary to probability that they must await confirmation by the discovery of a much better preserved skull. These questions of detail, if confirmed, will indicate the existence of another unexplained factor in the telescoping process. On the restorations of the skull, the maxillary is not

fastened to the braincase, but is represented as stopping at the level of the anterior margin of the frontal, with no part of this bone extending backward above the supraorbital process. According to this interpretation the rostrum was supported solely by the vomer and the ascending processes of the premaxillaries, which extend backward to the parietals, a mechanical arrangement that is not only improbable, but structurally defective. Professor Abel states that the postero-internal extremity of the maxillary stops at the antorbital line and does not push backward across the supraorbital process along with the ascending process of the premaxillary, but instead slides under the frontal. The last mentioned detail appears to be substantiated by the published photograph and would indicate that an infraorbital plate or process of the maxillary was present. If the contact between the frontal and maxillary has been correctly interpreted, the normal mammalian relationship of these bones has been retained, which furthermore is not materially different from the relations of these bones in *Eubalaena* and in the zeuglodont type of skull. Granting that the restoration represents the actual present condition of the specimen, there is no reason why the supraorbital process may not have been narrowly margined anteriorly by a thin plate of the posterior end of the maxillary, which was destroyed without leaving any trace, if the connection between these elements was so loose that no impression was made on the upper surface of the frontal. According to König (1911), who was the first to comment on this skull, its characters were not very different from those of *Agorophius*, on which the maxillary does overspread the supraorbital process. This observation is disputed by Professor Abel (1924). *Xenorophus* and *Rhachianectes* are the only known cetaceans in which it is apparent that the maxillary does not reach postero-internally as far back as the premaxillary, but on both of these skulls the maxillary has been thrust backward over the frontal. It is stated that the lachrymal can be seen from a ventral view in the antorbital notch, but this bone is not so indicated on any of the restorations. The dentition is still functional in *Patriocetus*, and the braincase is not materially unlike those of generalized toothed whales, but the periotic bone is of the mysticete type, with long apophysis wedged in between the exoccipital and squamosal. *Patriocetus* appears to be a late Oligocene survivor of an archaic family of cetaceans that preceded the cetotheres. It is more than likely that future discoveries will show that this family contained types directly related if not ancestral to the succeeding edentulous cetotheres.

MYSTICETI

As a basis for an interpretation of the developmental history of the true mysticetes we have seven genera of living whalebone whales and a rather large number of fossil species ranging in age from Upper Oligocene to and including the Pleistocene. Many of them, however, are based on very scanty remains. Starting with the more generalized cetacean skull on one hand and ending with the modernized mysticete on the other, it becomes apparent that the possibilities for remodeling are limited to certain definite details and that the fossil types represent successive stages in the developmental history of several phyla. If we based our deductions solely on a critical comparison of the Austrian Upper Oligocene and the Patagonian Lower Miocene mysticete skulls, we should be led to assume that the forward overthrust of the posterior occipital elements had precedence over the

backward interdigitation of the median rostral elements. Nevertheless, skulls of Miocene cetotheres from later geological stages do not lend any support to this assumption, for *Cetotherium* and related genera exhibit a less advanced stage in the forward overthrust of posterior occipital elements and a pronounced inter-

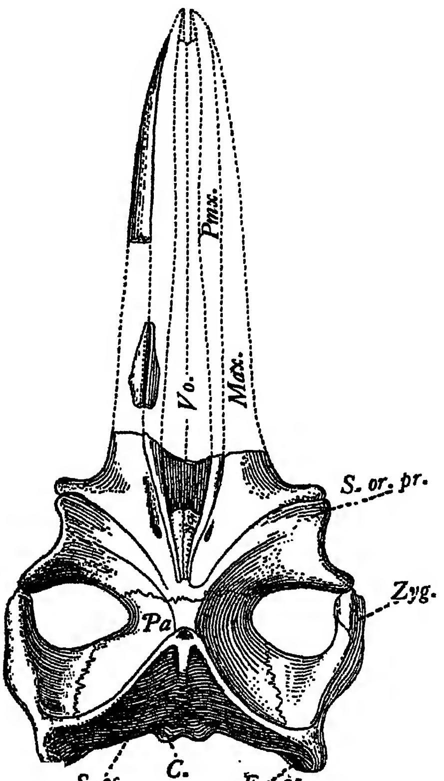


FIG. 17. DORSAL VIEW OF SKULL OF CETOTHERIUM RATHKII, UPPER MIOCENE, RUSSIA (After Brandt)

digitation of rostral and cranial elements. It is obvious that our available material is too meagre for more than vague generalization on the lines of descent and that any discussion of the history of the mysticetes must be confined to types arbitrarily selected to illustrate certain features of this general evolutionary process. There is evidence that several phyla of cetotheres advanced along similar lines. In one direction there is a persistence of the dominant forward overthrust of posterior occipital elements, and an absence of rostral and cranial interdigitation. This is the type of remodeling that led up to the modernized balaenids. In the other direction, the forward overthrust of the posterior occipital elements was coupled with a backward interdigitation of the median rostral elements, as a result of which the postero-internal extremities of the maxillaries, the premaxillaries, and the nasal bones became suturally united with the frontals on the vertex of the interorbital region. Some of the extinct cetotheres and all of the living balaenopterine whales exhibit this type of telescoping. Various intermediate stages of these two general trends occur among the cetotheres.

BALAENIDAE

Winge (1918) was the first to suggest that the balaenids represent the most primitive known mysticetes, although at the time this was written no right whales older than Pliocene had been described. That the Balaenidae were already differentiated as a family before the Lower Miocene is made certain by the occurrence of an already specialized form, *Morenocetus parvus* (Cabrera, 1926), in the Patagonian marine formation of Chubut, Argentine Republic. The dominant forward overthrust of the posterior cranial elements has carried the apex of the supraoccipital shield to the anterior interorbital region, excluding the parietals from the vertex of the skull, and reducing the median exposure of the frontals to a narrow strip behind the nasal bones. The sutures show that the nasal bones, the premaxillaries, and the maxillaries occupied the usual balaenid position

anterior to the supraorbital processes. The latter slant backwards and slope from the interorbital region to the rim of the orbit. The subsequent developmental history of this family during the Miocene is unknown. Several types of more highly specialized balaenids such as *Balaenula balaenopsis* (Van Beneden, 1878) make their appearance during the Pliocene, and their successors are the living genera that comprise the family Balaenidae.

NEOBALAENIDAE

In the progressive specialization and differentiation of the balaenid stock, two or more trends of development were followed, one of which resulted in the elongation and lateral compression of the rostrum as seen in the Balaenidae and the other by a retention with very little modification of the early cetothere type of rostrum. The living pigmy whale (*Neobalaena marginata*) belongs to the latter group. The rostrum of this whale is very little longer than the occipital shield and tapers rapidly from a broad base to a slender tip. The mandible is unusually robust and is strongly bowed outward. The skeleton of this whale has more peculiarities than any other living mysticete. It has 17 pairs of large broad ribs, of which at least eight are not articulated. The seven cervicals are completely fused with one another. There are 18 dorsal vertebrae, but no ribs are attached to the first of the series. The lumbar vertebrae have been reduced to one or two, and the caudals do not exceed 14 in number. Future discoveries of fossil mysticetes in the New Zealand and Australian region should throw much light on the developmental history of *Neobalaena*, which seems to be an offshoot of some early stock that passed through its development in the Southern Hemisphere, following a somewhat different path from the balaenids, and acquired peculiarities in the form of the ribs, the vertebral column, and the hand.

CETOTHERIIDAE

If we take their features seriatim, we find that the skulls of all known edentulous Miocene cetotheres have supraorbital processes that slope gradually outward from the dorsal surface of the interorbital region to the rim of the orbit and are never abruptly depressed basally below the level of the former as in the balaenopterine whales. Many of these cetotheres retained a well defined intertemporal region, constituted entirely by the parietals, which meet along the median line in front of the supraoccipital shield. In most species the braincase is short and broad, but the supraoccipital shield is quite variable in shape and extent, depending in part upon the degree of forward overthrust. The narrow ascending process of the maxillary is suturally united with the mesial projection of the frontal. The general arrangement of the bones that inclose the narial passages is more nearly in agreement with the typical structure of terrestrial mammals than with the toothed whales. The nasal bones and mesial projections of the frontals completely roof over the ethmoid region and the dorsal nasal cavity, and in addition the palatine is excluded from the anterior wall of the corresponding narial passage. The choanae lie behind the anterior opening leading to the nostrils, and the infraorbital plate of the maxillary is retained.

The skull of the Upper Oligocene *Cetotheriopsis lintianus* (Meyer, 1849; Brandt, 1873), found near Linz in Austria, is characterized in part by a high narrow triangular supraoccipital shield, which curves more forward than upward and is divided mesially by a long vertical

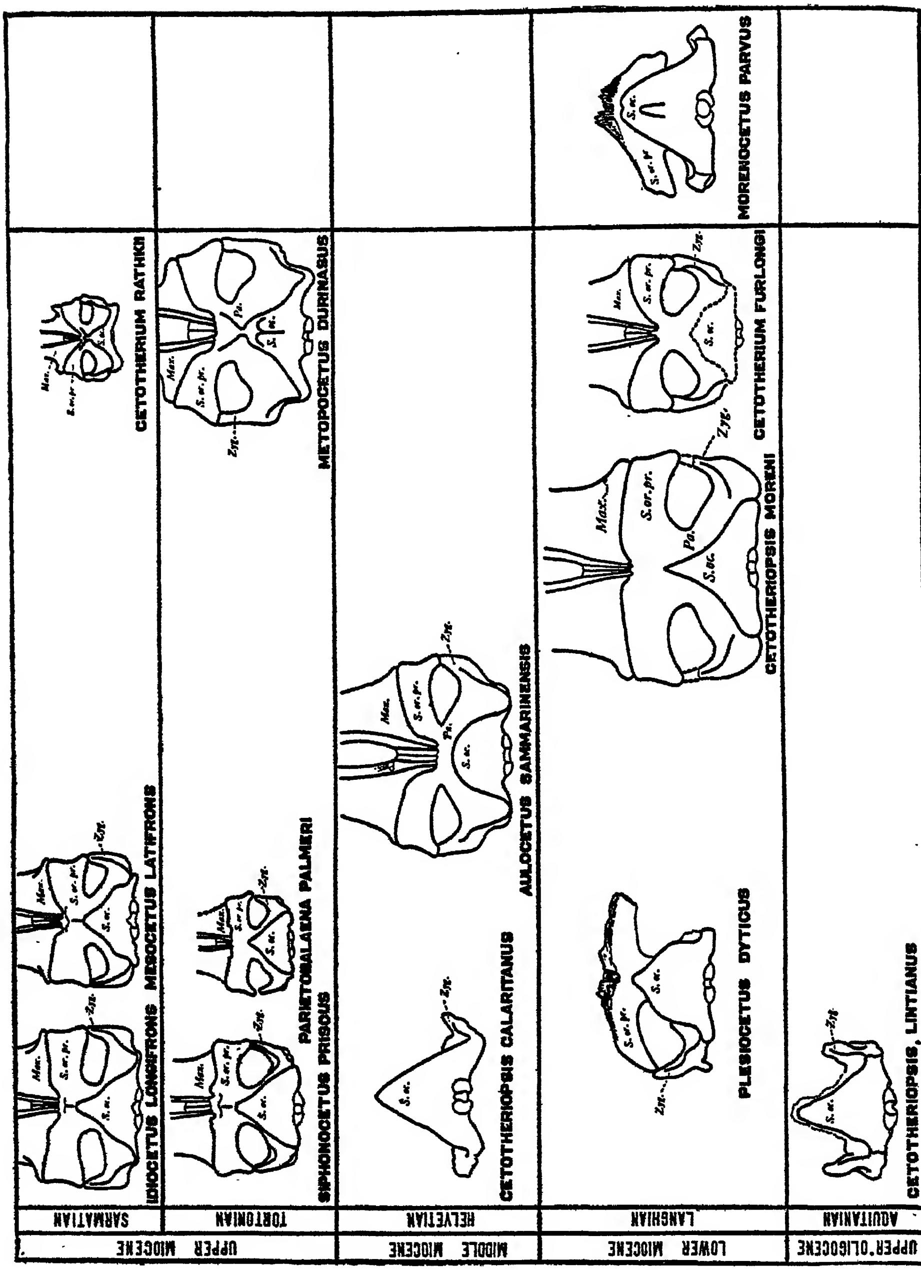


Fig. 18. Diagram Illustrating Stages of Telescoping in Existence during the Miocene in the Families Cetotheriidae and Balaenidae

carina; elongate zygomatic processes, which do not reach forward to the level of the apex of the supraoccipital shield; and the vertex of the braincase as viewed from behind is strongly depressed below the arching lambdoid crests. This imperfect cetothere skull is quite important, for it demonstrates that telescoping was an accomplished fact by the close of the Oligocene and that an advanced stage in the forward thrust of posterior occipital elements, such as is found in *Cetotheriopsis*, must have been preceded by developmental stages that led up to this type of telescoping. The Oligocene period unquestionably witnessed great elaboration of the telescoping process in the cetotheres, but unfortunately their known fossil remains are so scant that they give us no clew as to how this extraordinary condition came about. The scarcity of fossil cetaceans in Oligocene formations seems all the more surprising in view of the wide variety of types that make their appearance in formations of Lower Miocene age.

Two distinct types of cetothere skulls from the Lower Miocene Patagonian marine formation of Chubut Territory, Argentine Republic, have been obtained. One of these, *Cetotheriopsis moreni* (Lydekker, 1894), consists of a skull measuring 74 inches in length, a mandible, tympanic bullae, and vertebrae. Though originally assigned to the genus *Cetotherium* it is obvious that this allocation is incorrect, as is evidenced by the absence of anterior temporal crests, the extreme flatness of the cranium, the triangular supraoccipital shield extending forward beyond the level of the posterior margins of the supraorbital processes, the very broad maxillaries, and the elongated nasal bones situated almost entirely anterior to the preorbital angles of the supraorbital processes. This cetothere is tentatively referred to the genus *Cetotheriopsis* on account of obvious similarities in the development and extent of the supraoccipital shield. Cetothere skulls with supraoccipital shields of similar proportions also occur in more recent geological stages.

The other Patagonian skull "*Plesiocetus*" *dyticus* (Cabrera, 1926) exhibits a second type of occipital shield. The inclination of the supraorbital processes appears rather unusual at first sight, but this abnormality is largely the result of distortion from rock pressure. The supraoccipital shield is distinctly constricted near the apex. As compared with *Cetotheriopsis moreni* the braincase is narrower at the base, the shield is more rounded, and the lambdoid crests are more salient, but the vertex is depressed as in the former. The forward movement of the supraoccipital pushed the parietals in front of it, so that they overspread the posterior borders of the frontals in the interorbital region. The sutures on the anterior borders of the frontals indicate that the nasal bones and the median rostral elements were slightly interdigitated with the cranium. The extent of the forward overthrust of the supraoccipital shield and the backward interdigitation of the mesial portion of the rostrum, the unusually slender supraorbital processes, the position of the nasal bones, as well as the relations of the bones in the intertemporal region show that this cetothere represents another advanced stage in the telescoping of the mysticete skull.

In one or more phyla of mysticetes the telescoping of the skull seems to have been largely limited to a forward movement of the posterior cranial elements, for the interdigitation of the rostral and cranial elements is very slight. This condition prevails in skulls of the Helvetian "*Mesocetus*" *hungaricus* (Kadic, 1907)

and the Tortonian *Siphonocetus priscus*, and *Parietobalaena palmeri* (Kellogg, 1924), on which the nasal bones, the premaxillaries, and the rudimentary postero-internal extremities of the maxillaries, while suturally united with the mesial projections of the frontals, are situated for the most part anterior to the level of the preorbital angles of the supraorbital processes. The apex of the supraoccipital shield extends forward beyond the extremities of the zygomatic processes and the posterior margins of the supraorbital processes. The frontals are broadly exposed in the interorbital region, and the parietals are shoved forward across the frontals, meeting on the mid-line to form a short sagittal crest.

The interdigitation of the rostral and cranial portions of the skull, in so far as substantiated by described specimens, is first observed in the Lower Miocene "*Cetotherium*" *furlongi* (Kellogg, 1925), which was found in Monterey County, California. The backward interdigitation of the mesial portion of the rostrum carried the ascending processes of the maxillaries and the premaxillaries, as well as the nasal bones, beyond the level of the preorbital angles of the supraorbital processes. In consequence of this backward movement, the facial portion of the skull becomes "dished in" mesially in some of the succeeding cetotheres, the anterior borders of the supraorbital processes curving forward and outward. The Tortonian *Cephalotropis coronatus* (Case, 1904), the Anversian *Mesocetus longirostris* (Van Beneden, 1886), and the Sarmatian *Cetotherium rathkii* (Brandt, 1873), and *Cetotherium helmersenii* may be cited as examples of this stage in the telescoping process. Some of these species were no larger than the new-born young of living finbacks.

Skulls of species referable to the Miocene genus *Cetotherium* were characterized in part by forward curving supraorbital processes, by the facial position of the nasal bones, by anteriorly directed zygomatic processes with peculiar elongated glenoid articular surfaces, as well as by long slender mandibles. A peculiarity that distinguished *Cetotherium* and related genera from other Miocene cetotheres is the presence of a sharply defined anterior temporal crest, which seems to foreshadow the abrupt depression of the basal portion of the supraorbital process seen in balaenopterine whales. Cetotheres belonging to this small group likewise possess the least modified braincase, for the parietals come in contact with each other in the intertemporal region, and the apex of the supraoccipital shield lies behind the level of the supraorbital processes.

The interdigitation of the rostral and cranial elements is well marked in a mysticete from Monte Titano, San Marino, Italy, which Capellini (1901) named "*Aulocetus*" *sammarinensis*. The formation from which this specimen was obtained has been allocated by some geologists to the Langhian stage and by others to the Helvetian. The narrow nasal bones have not been shortened, although they lie almost entirely behind the level of the preorbital angles of the supraorbital processes of the frontals, and are as long as or longer than the breadth of the extremities of the latter. A short intertemporal region with broad sagittal crest is retained, and the apex of the rounded supraoccipital shield is not extended forward to the level of the extremities of the outward bowed zygomatic processes.

In the preceding brief résumé of the cetotheres the writer has endeavored to select types that show the main structural features of their evolutionary history, and many equally important species have been omitted. Capellini, Strobel, Portis,

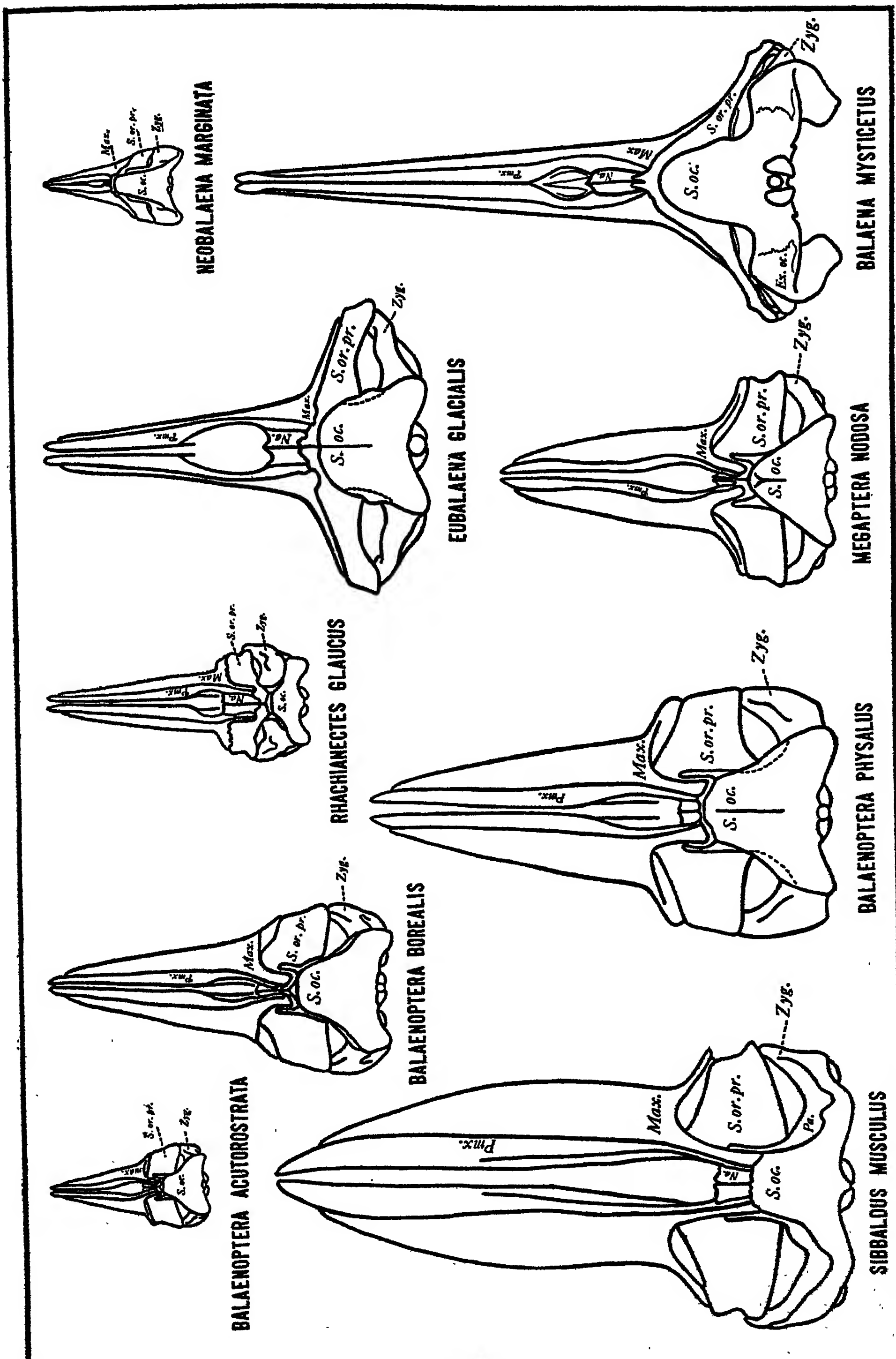


FIG. 19. DIAGRAM ILLUSTRATING STAGES OF TELESCOPING REPRESENTED AMONG LIVING MYSTICETI

and Brandt have figured and described a rather large number of cetotheres from Italy and southern Russia. Conditions for the preservation of the mysticetes apparently were more favorable in Belgium than elsewhere, for the largest faunas of extinct cetotheres of Upper Miocene and Lower Pliocene age thus far known occur in the Antwerp Basin, and these species are exceptionally well illustrated in the memoirs of Van Beneden (1885–1886). Many of the Upper Miocene cetotheres from the Atlantic coastal plain described by Cope are figured by Case (1904).

RHACHIANECTIDAE

On comparing the diagrams of the skulls of living mysticetes it will be seen that *Rhachianectes* (Andrews, 1914) stands apart from other whalebone whales, and is the least modified, and furthermore that the conditions observed are readily derivable from the cetothere skull. There is a well marked interdigitation of rostral and cranial elements, the base of the supraorbital process is abruptly depressed below the dorsal level, the overthrust of the supraoccipital shield has not advanced far enough to eliminate the interparietal, although the parietals are pushed apart, and the frontal bones are broadly exposed in the interorbital region.

BALAENOPTERIDAE

In North America and elsewhere we observe that the modernized types make their appearance toward the close of the Miocene, and that the Upper Miocene witnessed the reduction and extinction of many of the types that preceded them. For a while the cetotheres continued to exist in diminished numbers, but they seem to have disappeared by the close of the Pliocene. The appearance of modernized mysticetes in the Upper Miocene was not unexpected in view of the previous history of the group. The whalebone whales found in the Upper Miocene diatomaceous earth of California are unmistakably modernized types and show the cumulative effects of specialization. All of the mysticetes obtained from the diatomaceous earth series exhibit affinities more or less remote with species now living in the Pacific Ocean. Extinct balaenopterine whales with skulls as large as any of their living relatives have been excavated in this earth. The little finner, *Balaenoptera ryani* (Hanna and McLellan, 1924), appears to be related to the living sharp-head finner whale, *Balaenoptera davidsoni*. The telescoping of the occipital and facial portions of this skull has not advanced as far as in the living species, but otherwise the resemblance is remarkably close. Although *Megaptera miocaena* (Kellogg, 1922) appears to be related to the existing Pacific Humpback whale, *Megaptera versabilis*, the interdigitation of the rostral and cranial elements of the skull is not as far advanced, but the forward overthrust of the supraoccipital shield has reached an extreme stage in this process.

As early in geological time as the Pliocene, the forward movement of the posterior occipital elements had reached an extreme stage in one or more extinct species of the genus *Balaenoptera*. The skull of the Pliocene *Balaenoptera cortesii* (Portis, 1885, pl. 3, fig. 35) from Montafia, Italy, exhibits a more pronounced forward overthrust of the elongated triangular supraoccipital shield than in any other known fossil or living balaenopterine whale, but it retains the slender outbowed zygomatic processes of the earlier cetotheres. Other extinct species of balaenopterine whales not unlike those now living have been found in deposits of Pliocene age in Belgium (Van Beneden,

1882) and Italy (Portis, 1885). One of the most complete Pliocene balaenopterine skulls in existence was found in 1806 on Monte Pulgnasco, Italy, in blue clay of of Plaisancian age and it, *Balaenoptera cuvieri* (Van Beneden, 1875), bears the name of the famous French palaeontologist, Baron Georges Cuvier.

MORPHOLOGICAL PECULIARITIES OF THE MYSTICETES

In spite of the extraordinary remodeling of the skull, the mysticetes (True, 1904) have retained many primitive features that are no longer found in odontocetes. The relations of the bones in the region of the narial passages are essentially normal, and the choanae lie behind the opening leading to the blow holes. The proximal ethmoid region and the dorsal nasal cavity are completely roofed over by the nasal bones. A separate lachrymal bone is retained, but the lachrymal duct has disappeared. The palatine is excluded from the anterior wall of the narial passage. It has increased in size and has been forced backward, pushing the pterygoid behind it. The most extreme stage of the mysticete type of telescoping is seen in *Sibbaldus*, in which the forward overthrust of the shield has carried the apex of the supraoccipital to the nasal bones, and the parietal sends forward a thin plate, which is applied to the lateral surface of the ascending process of the maxillary above the abruptly depressed base of the supraorbital process. The interlocking of the rostrum with the cranium is more obvious than in any other balaenopterine whale. In *Neobalaena* and *Balaena* the forward overthrust of the supraoccipital shield has gone a step further, and its apex lies considerably anterior to the preorbital angles of the supraorbital processes. In *Balaena* and *Eubalaena* the lateral compression of the rostrum is very conspicuous. A pterygoid fossa for an accessory air sinus has been formed in front of the inner ear. The balaenid and balaenopterine whales have a similar type of scapula, with large functional acromion and coracoid processes. These processes are reduced to mere tubercles in the scapula of *Megaptera*. The primitive condition of the elbow and wrist joints has been lost. The carpus in *Balaena* is immovable and broad, and conspicuously lengthened in *Megaptera*. The lumbar vertebrae are furnished with widely projecting transverse processes. The ribs exhibit a tendency to restrict their connexion with the thoracic vertebrae and with the atrophied sternum, which consists of the manubrium alone. The ribs of living mysticetes are single-headed in contrast to the normal type of rib found in some of the cetotheres. Considerable remnants of the hind limb are retained, including the rod-like pelvis, the atrophied femur, and in some cases a vestige of the upper end of the tibia. The caudal vertebrae acquire large centra with broad flattened transverse processes to conform to the manner in which the tail is wielded.

We have seen that the early cetotheres lost their teeth and acquired two rows of blade-like plates of baleen depending from the roof of the mouth, which served as a seine when the animal was feeding. Small crustaceans or fish constitute the food of the living whalebone whales, and the cetotheres no doubt subsisted on the same types of food. In the living mysticetes the prey is engulfed in the oral cavity along with a large quantity of water, which necessarily must be expelled by the tongue before such small prey can be swallowed. Hence these plates of baleen with internal marginal fringes of intermatted bristle-like fibers form a strainer remarkably well adapted for

taking surface-swimming crustaceans or for impounding small fish, which are scooped up by the animal when plunging forward with mouth open. The capacity of the mouth was increased in two ways. In the balaenids it has been accomplished by arching the upper jaws and in the others by a bowing outward of the lower jaws in conjunction with a broadening of the rostrum. Surprising as it may seem four barrels of shrimps were taken from the partially filled stomach of a huge blue whale (Andrews, 1916), whose throat measured about 9 inches in diameter.

It is worth while then to explain just what has been accomplished by the remodeling of the generalized mysticete skull. This brings us around again to a comparison of living and extinct types. In general it may be stated that the forward movement and expansion of the supraoccipital shield was followed or accompanied by a broadening of the base of the skull. This forward overthrust of the posterior occipital elements also changed the relative positions of the zygomatic processes, for they become more robust and their articular surfaces come to lie near the level of the occipital condyles. The mouth cavity increased in size, and this in turn permitted a lengthening and expansion of the blades of baleen that hang from the roof of the mouth. The mandibles acquired a disproportionately large size in comparison with the braincase, becoming bowed outward and loosely connected anteriorly. The symphysis disappeared, and the ligaments that bind the articular head of the mandible to the glenoid articular surface developed the strength necessary to bear the great weight of the outbowing lower jaws. The opening leading to the nostrils or "blow holes" was drawn backward in proximity with the anterior wall of the braincase. The posterior position of the blow-holes permitted exhalation and inhalation without elevation of the muzzle above the water level, which was rendered difficult, if not impossible, by reason of the inflexibility of the neck. The increase in the size and proportions of the skull, the outbowing of the lower jaws, and the development of long blades of baleen attached to the roof of the mouth, required a firm socket to support the enormous increase in the weight of the head suspended from it. This result could be secured by the development of massive cervicals, or by the shortening of the neck and by the ultimate fusion of the seven cervicals into a compact mass as in *Balaena mysticetus* and *Eubalaena glacialis*. The ankylosis of the cervical vertebrae and their fusion into a compact immovable mass is believed to be the culmination of this evolutionary trend. In the case of any pelagic mammal having feeding habits similar to those of the whalebone whales, flexibility of the neck would be a mechanical weakness; hence the short neck appears to fulfill the necessary requirements for cetaceans with relatively large skulls. The basicranial region was largely protected from telescoping by the relations of the maxillary and frontal, and consequently the nasal cavity retains a cribriform plate with passages for the olfactory nerves as well as remnants of the turbinated bones, including the ethmoturbinals.

It must be understood that this summary attempts to account merely for the general features of the evolutionary history of the mysticetes, and that a late stage in this process may appear at an early geological time or an early stage may persist to the present day. The skull of the living gray whale (*Rhachianectes glaucus*) is constructed along the lines of an early stage and has been called a living fossil. Conversely the skull of the Lower Miocene *Morenocetus parvus* has already acquired

many peculiarities of detail that represent a late stage of the telescoping process.

Recent studies by Ridewood (1922) on embryo skulls of highly telescoped mysticetes confirm in a large measure the general features of the palaeontological evidence. Skulls of embryos exhibit a rather broad intertemporal region formed by the parietal bones. An interparietal bone has been observed in the skull of a 9 inch foetus of *Balaenoptera acuto-rostrata* and in a foetus of *Balaenoptera borealis* measuring 3 feet 6 inches in length. No sign of an interparietal bone was observed in the skull of a foetus of *Sibbaldus musculus* measuring 6 feet 4 inches in length or in one of *Megaptera nodosa* measuring 27 inches in length. In all of the above mentioned embryo skulls, the parietal bones have been pushed forward across the frontals.

Embryology also furnishes the evidence that the progenitors of the mysticetes were provided with teeth. As many as 40 or even more minute teeth with pin-like crowns may be found hidden in the gum on the maxillary of a foetal mysticete, but they are soon resorbed. The atrophy of the teeth was followed by the growth of papillae (Tullberg, 1883) along the outer margin of the upper jaw, and these developed into a series of crosswise placed corneous blades, the baleen. An inquiry into the morphological features of the mysticetes leads one to the conclusion that many of the peculiarities of detail were adjustments to unexpected conditions associated with the procurement of food. An abundance of soft-bodied crustaceans provided ample and readily obtainable food, which required no mastication, but which did require some structure adapted for catching such minute prey. The blades of baleen are remarkably well adapted for this purpose, and the remodeling of the skull seems to have been profoundly influenced by their development.

ANATOMICAL AND PHYSIOLOGICAL ADJUSTMENTS

Adaptation to life in the water has brought about many changes, as already indicated, in the bodily organization of cetaceans. We observe that the motive power was transferred from the limbs, which originally served as ambulatory organs, to the hinder end of the body, resulting in the development of caudal flukes, which became the propelling mechanism; the hind limbs disappeared; and the fore limbs were modified into fin-like organs, which served as rudders. This adaptation is not a comparatively recent biological phenomenon, for a similar remodeling of the skeleton in a group of marine reptiles, the ichthyosaurs, took place at an earlier period in the earth's history. Convergent developments of independent origin such as these indicate that the remodeling of the skeleton was governed by the operation of some general principle of aquatic adaptation.

Flippers of whales bear little resemblance to the fore limbs of land mammals, for they are overlain with blubber and are fashioned like a paddle with margins hardened by fibro-cartilage. Nevertheless they are supported and constructed with similar bones, muscles, blood vessels, and nerves. The hand has been remodeled to conform to the use to which it is put. The wrist bones have lost their original shape and occasionally fuse into a compact mass in old individuals. There has been a reduplication of the bones in the fingers, which has been variously explained as the result of a secondary division of the strand of cartilage attached to the terminal phalanx, of intercalary syndesmoses, or of double epiphysis formation (Küken-

thal, 1891). In the typical mammalian hand the number of phalanges in each finger does not exceed three, whereas as many as seventeen have been observed in foetuses of *Globicephala*. Whalebone whales apparently lack the thumb, but it is present in the toothed whales. The chief function of the flippers is to enable the whale to descend or ascend, or to turn sideways. They are used mainly for steering and balancing, and have lost their former rowing function. The propelling mechanism of a whale is centered in the powerful flukes at the end of the tail, and the muscles and tendons that control these organs of propulsion act as levers, which pull them in an up and down direction. The greatest velocity is produced by alternate upward and downward strokes of the flukes. When proceeding at a slower speed the flukes cut the water laterally and obliquely downward.

Less striking physiological phenomena have been observed in the thermal adjustments. Since the capacity of water for conducting heat is 27 times as great as that of air, whales would lose a vast amount of body heat were it not for the presence of a blanket-like heat-retaining layer of fat over the whole body and the absence of sweat or sudoriferous glands. Whales in tropical waters need this protection nearly as much as those in temperate or cooler water, for the individual body temperatures of whales are higher than the water they frequent. The body temperature of the Sei whale (*Balaenoptera borealis*) is between 95° and 97°F., and that of the common harbor porpoise (*Phocaena phocoena*) is 96°F.

The hide of whales is endowed with certain histological and structural features that afford the maximum elasticity, and conversely are capable of retarding increasing compression on the thorax. The fibrous blubber has tremendous strength and tenacity, for it will resist a strain of several thousand pounds. Finbacks have been known to drag a ship when the prongs of the harpoon were merely caught under the blubber on the back.

Adjustments and modifications in the structures that function in the process of breathing were necessary to permit feeding below the surface. Water would surely get into the lungs during swimming with a wide open mouth were it not for the fact that a whale's narial passages do not open into the throat as in land mammals. A continuous tube between the narial passages and the trachea or windpipe is formed by an elongation of the arytenoid cartilages and the epiglottis, which fits into the soft palate. Other anatomical and physiological adjustments have come about to permit sustained submergence. Whales can remain submerged for varying lengths of time, as a rule from 7 to 15 minutes, but in case of necessity for 2 hours (Lillie, 1915). Prolonged submergence requires an adequate supply of oxygenated blood, but it is also true that the compression of the gases in the lungs would raise the partial pressure of the oxygen in the alveoli so that practically all of it could be consumed. Some provision has also been made for the absorption of the accumulated carbon dioxide.

The closing apparatus of the nose is equally interesting, for closure is accomplished in an entirely different manner in the two groups of living whales. The toothed whales have a single external nostril, while the whalebone whales have a double nostril. In the case of the toothed whales the narial cavity is divided into a series of pockets into which the narial passages open, and between these pockets are a series of plugs controlled by muscles that apparently contract when pressure is exerted on the

external flap of fibro-elastic cartilage that covers the external nostril. Returning to the whalebone whales we observe that the tubular narial passages slope forward and upward, and are furnished with spiral folds that fit into one another when pressure is exerted from without. Although the closing mechanism is constructed along different lines in the two groups, in both the nostrils are effectually closed when the animal is submerged.

VISUAL SENSE

Most whales have such acute powers of hearing that it is an open question whether they see or merely hear objects that attract their attention. Nevertheless we have indubitable evidence that the eyes of cetaceans are adjusted to the specific functions they have to perform. In its gross features the whale eye differs from that of a land mammal in having the eyeball immovable, eyelids without eyelashes, no tarsus or supporting cartilage in the eyelid, no Meibomian glands, and a downward direction of the eye axis. As a result of an aquatic mode of life whales have acquired a more spherical lens and a greatly thickened sclera. The ciliary processes and their muscles are reduced in size and have lost their original function of controlling the shape of the lens. The tension of the suspensory membrane (the *zonula zinnii*) is not great enough to flatten the anterior surface of the lens, and as a general rule the latter retains a more or less spherical shape. Whales thus lack the power of accommodation.

Since the functional irritant for the dioptrical or recipient apparatus of any mammal is light, to function correctly the eye must be constructed so that clear cut pictures are formed on any spot of the retina. Inasmuch as the refractive index of sea water is not the same as that of air, the eyes of whales must be adjusted to function when immersed. There is so little difference in the refractive indices of sea water and of the aqueous humor that the cornea is dioptrically inoperative when the eye is submerged, and the dioptric apparatus is thus reduced to the lens. To compensate for this (fig. 20, diagram 6), however, the curvatures of the anterior and posterior surfaces, as well as the axis or height of the lens and the refractive indices of the liquid media, have been corrected so that light rays passing through sea water are brought to a focus on the retina.

A number of investigators have pointed out that the eyes of many of our living land mammals do not possess the power of accommodation, and it is not unlikely that similar conditions prevailed among the animals of the past. Diagram 2 represents a normal or emmetropic eye, in which parallel rays of light reaching the eye through the air are brought to a focus on the retina. Now if a land mammal with an eye of this sort should be transferred to a pelagic habitat, its vision would be impaired, for only the outlines of objects viewed under water would be recognizable, because the light rays reaching the eye through sea water would be focussed beyond the retina (Diagram 3). Even with the maximum accommodation, in which the anterior and posterior surfaces of the lens have the same radius of curvature, parallel rays of light reaching the eye through sea water would be focussed beyond the retina. Unless the axis or height of the lens were increased and the refractive indices of the surrounding liquid media were altered slightly, the eye would function imperfectly when immersed in sea water.

Under atmospheric conditions the eyes of most whales are myopic, that is the

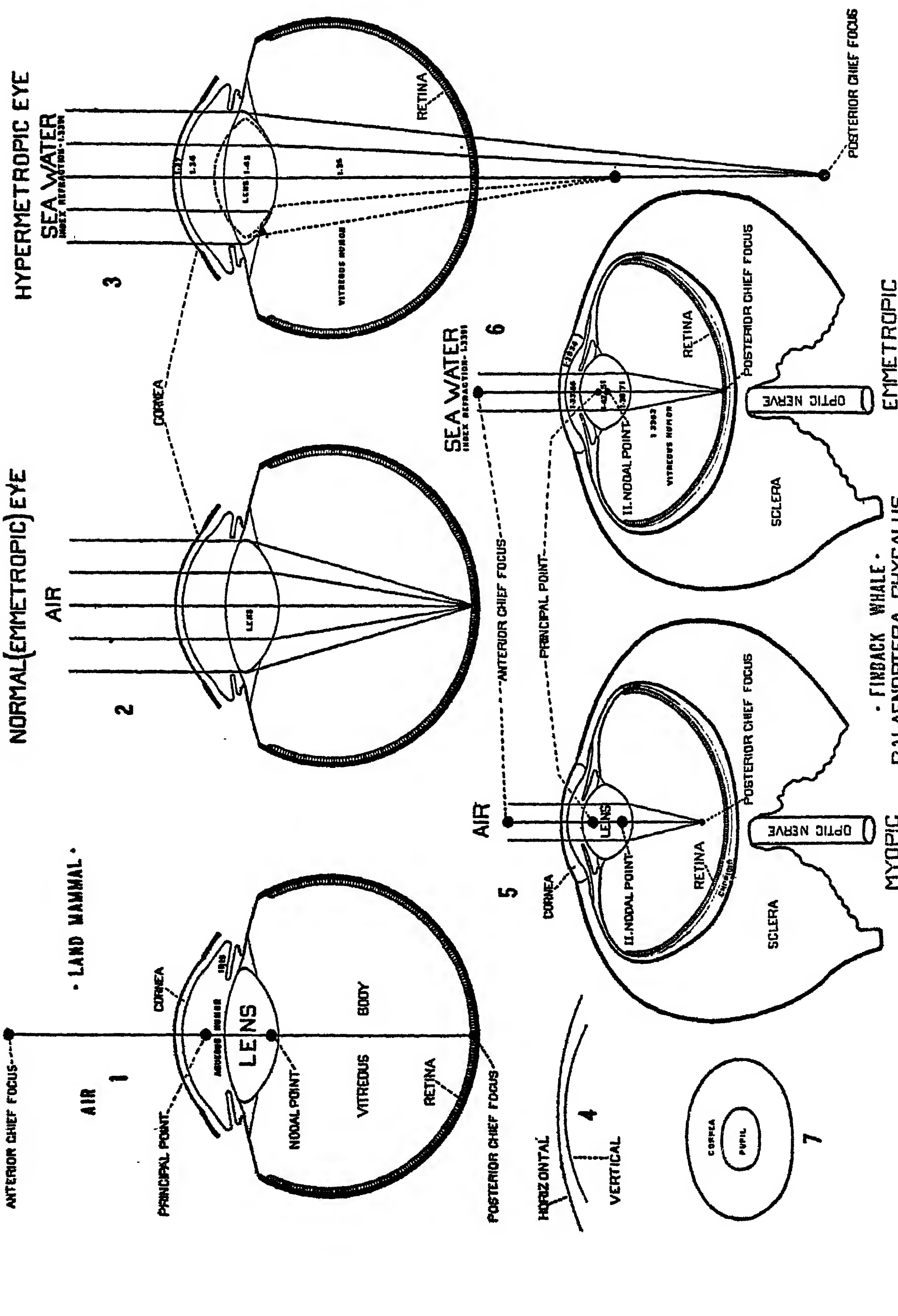


Fig. 20. Diagrams Showing Focal Points of Parallel Rays of Light Reaching the Eye through Air and through Sea Water

light rays are brought to a focus in front of the retina. Thus when a whale tries to view objects above the water level (Diagram 5) it is troubled not only with astigmatism because of differences in curvature of the cornea in the two directions (Diagram 4), but also in being unable to change the curvature of the lens for optical accommodation because of defective ciliary muscles. According to Matthiessen (1886–93) the cornea of a whale living in salt water functions like a weak dispersive lens and, although the curvature of the cornea has little optical significance, an increase in size brings more light through the pupil to the peripheral parts. From an optical standpoint it would be to the advantage of a whale to have a large cornea, for they have to see with a weak light when feeding below the surface. The deeper a whale dives the weaker the light it has to see by. There may be some question, however, as to the limits of vision in the inky darkness that prevails in the depths of the sea. The bottlenosed beaked whale (*Hyperoodon*), which hunts for cuttlefish in the depths of the ocean, has an eye with a more pronounced corneal curvature, which permits more light to reach the peripheral parts of the retina, and there is a corresponding thickening of the rim and its abutment, the sclera. A large cornea is disadvantageous to the whale for architectural and thermal reasons. The toothed whales have larger corneas than the whalebone whales, but this enlargement has been compensated by the thickening of the cornea itself.

Fossil casts or impressions of soft parts like the eyes are of very rare occurrence, so that for evidence in regard to the visual powers of the extinct Eocene zeuglodonts one must examine natural and artificial casts of the cranial cavities of their skulls. These endocranial casts furnish data on the proportions of the several parts of the brain and the relations of the nerves, and also afford much information about the sensory capacities of the animals in question. A number of these brain casts have been described by Fraas, Stromer, Elliot Smith, Andrews, and Dart. The most complete endocranial cast known to us at present was figured and described by Stromer in 1908.

Brains of late Eocene zeuglodonts appear shrivelled and shrunken in comparison with the earlier forms, and there is reason to believe that these animals had not such keen sight as some of their contemporary land dwelling allies. A relative loss of the faculty of sight appears to be indicated by the smallness of the cerebrum and its lack of growth in later forms. The side to side contraction of the area between the olfactory peduncles and the *tuber cinereum* demonstrates the relative atrophy of the optic chiasma in the zeuglodont brain. A reduction of the faculty of sight and possibly of smell involves a compensatory dependence by the zeuglodonts upon the sense of touch in the muzzle. This interpretation, according to Dart (1923), is suggested by the trigeminal specialization in the brains of zeuglodonts. One might infer from the known braincasts that these zeuglodonts experienced some difficulty in adjusting their eyes for under-water vision and that a defective eyesight may have been one of the causes that contributed to the final extinction of this widely distributed group.

In its general features, the cast of the brain of *Prosqualodon* (Dart, 1923) shows a remarkable resemblance to the zeuglodont type, particularly in the cerebellar enlargement and hypertrophy of the trigeminus. On the other hand the brain of *Prosqualodon* has a well defined

optic chiasma, and this area is expanded in contrast to the contracted zeuglodont brain. The widening of this area is correlated with elaborate visual capacities. The brain casts of other extinct Miocene porpoises show that the optic chiasmic region was well developed, and there is nothing to indicate that they differed to any marked degree from their living relatives so far as their visual powers are concerned.

As regards hydrostatic adjustments the whale eye has been adapted to withstand varying pressures as well as the impact of the water when speeding at the surface. It is a well known fact that a vault designed to withstand heavy pressures has to be built so that the directions of the stresses, strains, and pressure forces fall within the abutment. Pütter (1902) points out that the abutment in the whale eye is the enormously thickened sclera. Fluctuations in hydrostatic pressure result in corresponding changes in intraocular pressure. External pressure increases by one atmosphere for each five fathoms of depth. A blue whale (*Sibbaldus musculus*) carried a line straight down for 220 fathoms, where it would have to withstand a pressure of 45 atmospheres or 630 pounds per square inch, and it remained below the surface for 32 minutes. The bottlenosed beaked whale (*Hyperoodon*) and the sperm whale (*Physeter*) are said to descend half a mile and possibly a mile. Pressures at such depths are enormous. At half a mile the pressure is approximately 1178 pounds per square inch and at a depth of a mile about 2349 pounds per square inch.

The chemical adjustments of the whale eye are equally interesting. Constant chemical irritation resulting from contact with sea water necessitates certain adjustments to protect the eye from inflammation or even more serious injury. The tear gland does not secrete a watery liquid, for the eye is no longer in danger of drying up, but instead exudes a greasy substance to protect the cornea from the various chemical substances found in sea water. No trace of the sebaceous Meibomian glands has been found in the eyelids of whales. Furthermore in a number of whales the conjunctiva or mucous outside coating of the eye has been replaced by cornified epithelium. Since the whale eye is subjected to almost constant immersion in sea water of 3 to 4 per cent salt content it does not appear unreasonable to assume that these details represent an adjustment to chemical irritants.

Inasmuch as the cornea of the eye is in direct contact with the water, one might expect that the eye would be protected in some way against continuous cooling below normal body temperature, and curiously enough the freezing point of the liquid media in the whale eye (Sudzuki, 1924) is somewhat lower (Δ 0.66° to 0.72°) than in land mammals. The eye also seems to be sufficiently protected against variations in temperature by the natural replacement of the liquid in the anterior chamber, for inflow and drainage are equal, and the aqueous humor should be maintained at approximately the same temperature as the blood.

OLFACTORY SENSE

Chemical senses, like those of smell and taste, which are closely associated physiologically, require organs that differ considerably in structure and relations. The sense of smell plays an important part in the welfare of many mammals, but cetaceans apparently found less and less need for olfactory structures.

Stromer in 1908 described and figured an unusually complete endocranial cast (fig. 21) *in situ* in a zeuglodont skull from the Qasr-el-Sagha beds of the Fayum,

Egypt. Not merely the cast of the brain but also those of the cavities and sinuses in the region of the narial passages are exposed to view. It is obvious that the sense of smell was still of considerable importance to this zeuglodont, as is shown by the development and peculiar elongation of the olfactory peduncles, which are attached to the ventral surfaces of the cerebral hemispheres in the characteristic mammalian fashion. The rather smooth cerebral hemisphere, which is primarily an olfactory receptive mechanism, is quite different from the convoluted cerebrum of living odontocetes and mysticetes. Only one investigator has had the opportunity to study a series of endocranial casts of Middle and Upper Eocene zeuglodonts. On the basis of these casts, Dart (1923) has concluded that the brains of late Eocene zeuglodonts show that the loss of the sense of smell was gradual and that this loss was accompanied by an excessive development of the trigeminal apparatus, which in a pelagic mammal provides much more information concerning food and enemies.

The whalebone whales (Mysticeti) have olfactory structures, but the retention of the sense of smell may be due in a larger measure to the actual mechanical construction of the skull (see page 44, fig. 2) than to the need of such organs, for the olfactory structures seem to be adapted, as in terrestrial mammals, for smelling through the medium of air. Water never comes in contact with the sinuses in which the olfactory nerves are distributed, and no odors other than those conveyed by water could be recognized when the whales are feeding below the surface. We are therefore at a loss to conceive how cetaceans may smell through the medium of water, inasmuch as the olfactory nerves are distributed in a rather simple manner to the mucous membranes of the olfactory pouches, which hang downward from the dorsal walls of the narial passages. Each of these olfactory diverticula has a slit-like orifice.

The archaic toothed whales of the Upper Eocene have passages for olfactory

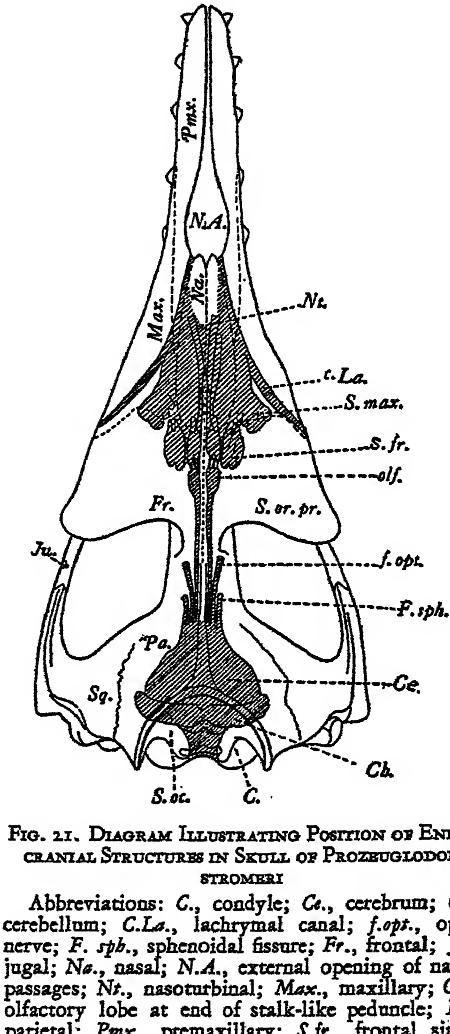


Fig. 21. Diagram Illustrating Position of Endocranial Structures in Skull of *Prozeuglodon stromeri*

Abbreviations: *C.*, condyle; *Ce.*, cerebrum; *Cb.*, cerebellum; *C.La.*, lachrymal canal; *f.opt.*, optic nerve; *F. sph.*, sphenoidal fissure; *Fr.*, frontal; *Ju.*, jugal; *Na.*, nasal; *N.A.*, external opening of narial passages; *Nt.*, nasoturbinal; *Max.*, maxillary; *Olf.*, olfactory lobe at end of stalk-like peduncle; *Pa.*, parietal; *Pmx.*, premaxillary; *S.fr.*, frontal sinus; *S.max.*, maxillary sinus; *S.oc.*, supraoccipital; *S.or.pr.*, supraorbital process of frontal; *Sq.*, squamosal.

nerves on the fore wall of the braincase. There may be some question as to the actual size of the olfactory orifices on the skull of *Xenorophus sloanii*, for the ethmoid

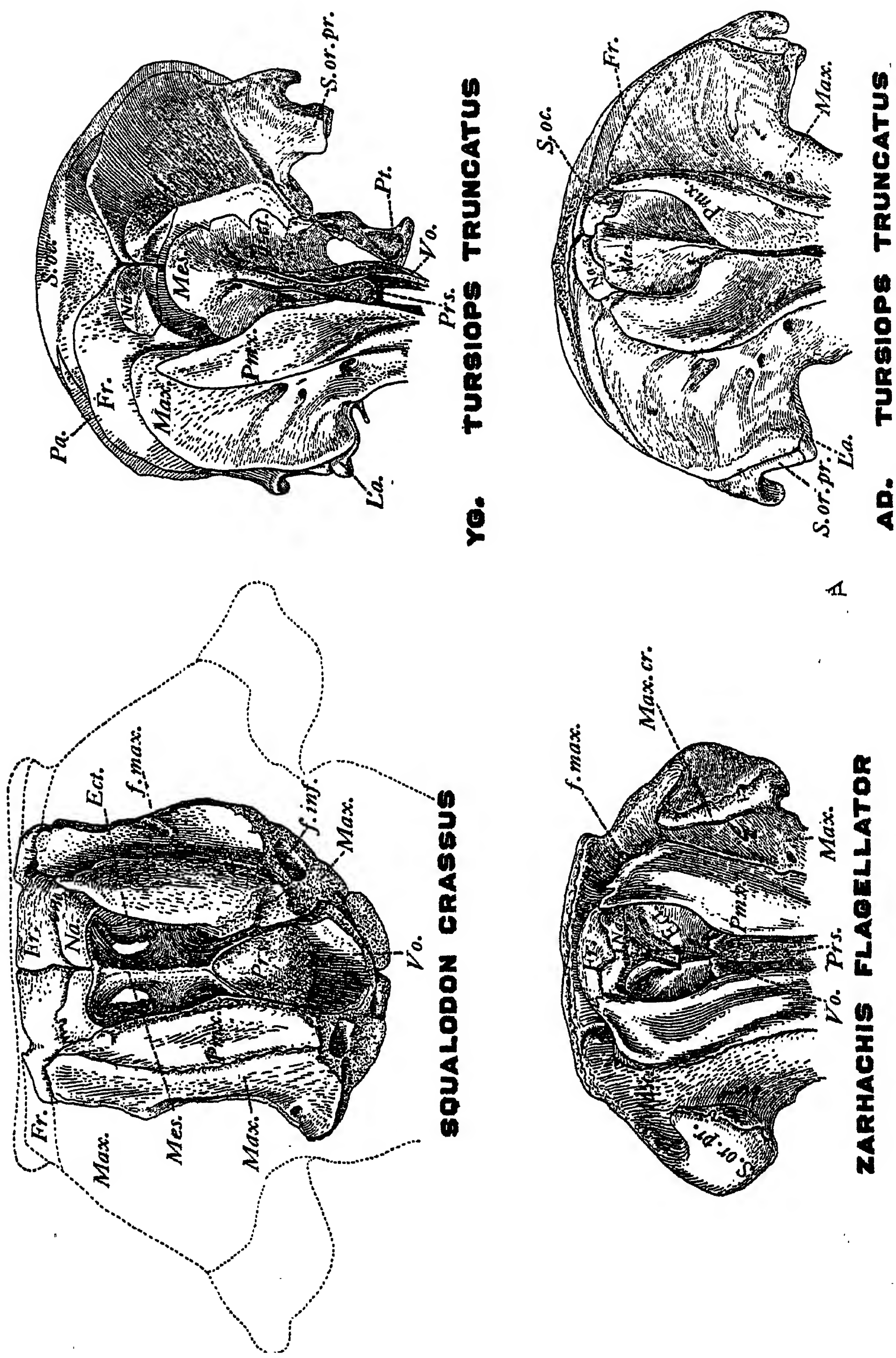


FIG. 22. FRONTAL VIEWS OF SKULLS ILLUSTRATING POSITION OF ETHMOID BONES IN SQUALODON CRASSUS, ZARHACHIS FLAGELLATOR, YOUNG TURSIOPS TRUNCATUS, AND ADULT TURSIOPS TRUNCATUS

bones are missing, but the fontanelle is quite large and the anterior wall of the braincase is unusually thick. The skull of *Archaeodelphis patrius* on the other hand has distinct nasal cavities in front of olfactory foramina of moderate size, which are set off from the forward sloping narial passages. The few endocranial casts of extinct odontocetes that have been described show that at the beginning of the Miocene the olfactory organs had dwindled to very small proportions as compared to *Prozeuglodon*. In the case of *Cyrtodelphis sulcatus* (Dal Piaz, 1905) and *Prosqualodon davidi* (Dart, 1923), the olfactory lobes are attached in a nipple-like fashion to the cerebral hemispheres and the insertion is somewhat higher than in "*Zeuglodon*." All of the squalodonts now known retained remnants of olfactory structures, if our interpretations of the foramina on the fore wall of the braincase are correct. Other extinct Miocene porpoises, including the primitive ziphioid types *Diochotichus* and *Squalodelphis*, have a pair of foramina on the anterior wall of the braincase for the passage of sensory nerves.

The living toothed whales have lost their olfactory organs, though such structures have been found in foetuses. Changes in the relations of the bones in the region where the olfactory nerves originally found passage have resulted in the closure of the opening in the cribriform plate and the concomitant lateral expansion of its component parts, the mesethmoid and ectethmoids, to completely cover the fontanelle on the anterior wall of the braincase between the medial margins of the frontal bones. Mechanical changes in the relations of the component parts of the odontocete type of skull appear to have restricted at first and finally prevented the physiological functioning of the olfactory apparatus. These changes have hastened the final reduction of the dwindling olfactory apparatus of the toothed whales. On the basis of skulls of Miocene porpoises, one would be led to conclude that the passages for the olfactory nerves were reduced by the upward and lateral expansion of the ectethmoids. In many of the late Miocene porpoises and in practically all of the living types, the mesethmoid and ectethmoids have fused to form a continuous sheet of bone, which overspreads the area between the nasal bones and the lateral margins of the trough-like vomer, forming the posterior wall for each narial passage. The general course of the reduction of the olfactory organs can be demonstrated also by comparison of brain casts of fossil porpoises from successive geological stages.

The position of the mesethmoid with reference to the frontals in certain well known types of extinct porpoises is especially instructive and furnishes data from which one may visualize the steps that culminated in the conditions found in skulls of living porpoises. The transition from one stage to another can not be traced at present in a single phyletic series, and recourse must be had to several unrelated types of porpoises. The brief review that follows is necessarily incomplete, but it seems likely that the changes in the relations of the mesethmoid and ectethmoids under discussion clearly indicate the successive stages in the closure of the foramina for the olfactory nerves.

In *Squalodon* the mesethmoid forms the most dorsal portion of the partition between the narial passages, divides the fontanelle between the frontals on the fore wall of the braincase into two large foramina through which the olfactory nerves pass and, extending upward, underlies the nasal bones and provides additional support for the vertex of the skull. The ectethmoids form the external surfaces

of the foramina for the olfactory nerves and overspread the internal borders of the more or less vertical surfaces of the frontals.

In the skull of *Zarhachis flagellator*, the mesethmoid likewise provides some support for the vertex of the skull, but each ectethmoid has grown around the passage for the olfactory nerve and has overspread the lateral surface of the mesethmoid, forming a crescentic foramen. The curved rostral edge of each ectethmoid is the original external edge, and at the caudal end of the foramen is the original internal edge. Succeeding stages in the telescoping of the odontocete skull brought about a further compression of the fore wall of the braincase, causing the mesethmoid to lose its original function of supporting the vertex, and ultimately it came to overspread the frontals below the nasal bones on the posterior wall of the narial passages. In skulls of living porpoises the plate-like bone that sheathes the anterior surfaces of the internal borders of the frontals, conceals the frontal fontanelle, and extends upward to overspread the lower borders of the nasal bones, unquestionably represents the combined mesethmoid and ectethmoids, and corresponds to the cribriform plate of other mammals. In most mammals, the ethmoid plate ossifies into a median mesethmoid bone bounded below on either side by the ectethmoids. These ethmoid bones comprise the cribriform plate, and in the early stages when the mesethmoid and ectethmoids are distinct the olfactory nerves pass out between them.

In a skull of a young *Tursiops truncatus*, the porous plug-like presphenoid rests in the trough of the vomer and the thin lateral walls of the latter embrace the lower half of this bone. Dorsally there is a second thin curved bone, coextensive with the internal and posterior walls of the narial passage, which fits into a groove on the upper margin of the thin lateral wall of the vomer and in addition sheathes the inner borders of the frontals outside the frontal fontanelle. One of these bones is present in each narial passage. These bones fulfill the requirements of the ectethmoids. The inner margins of the lateral plate-like ectethmoids do not meet the mesethmoid above the presphenoid as in an older individual. The mesethmoid no longer supports the vertex of the cranium and has been crowded out of its original position to overspread the anterior wall of the braincase below the nasal bones. Inferiorly on each side it has fused with the corresponding ectethmoid. On the internal margin of each ectethmoid is an incomplete fissure or vestigial foramen, which marks the original position of the orifice for the olfactory nerve. In older individuals these ethmoid bones completely fuse and form a continuous sheet of bone, which extends upward toward the vertex, overspreading the lower borders of the nasal bones. The olfactory nerves were thus effectively shut off from the narial passages by the development of this bony plate.

ACOUSTIC SENSE

Life in the water necessitated a remodeling of the organ of hearing so that it would function under the changed conditions. The initial stages in the transformation of an organ of hearing designed for the perception of air-borne sounds to one adapted to receive water-borne sounds are unknown, for the earliest known zeuglodonts have the osseous portions of this organ as highly developed as any of the living whales. The ancestors of the living cetaceans must have had functional ear drums just as have man and other mammals, but in the course of geological

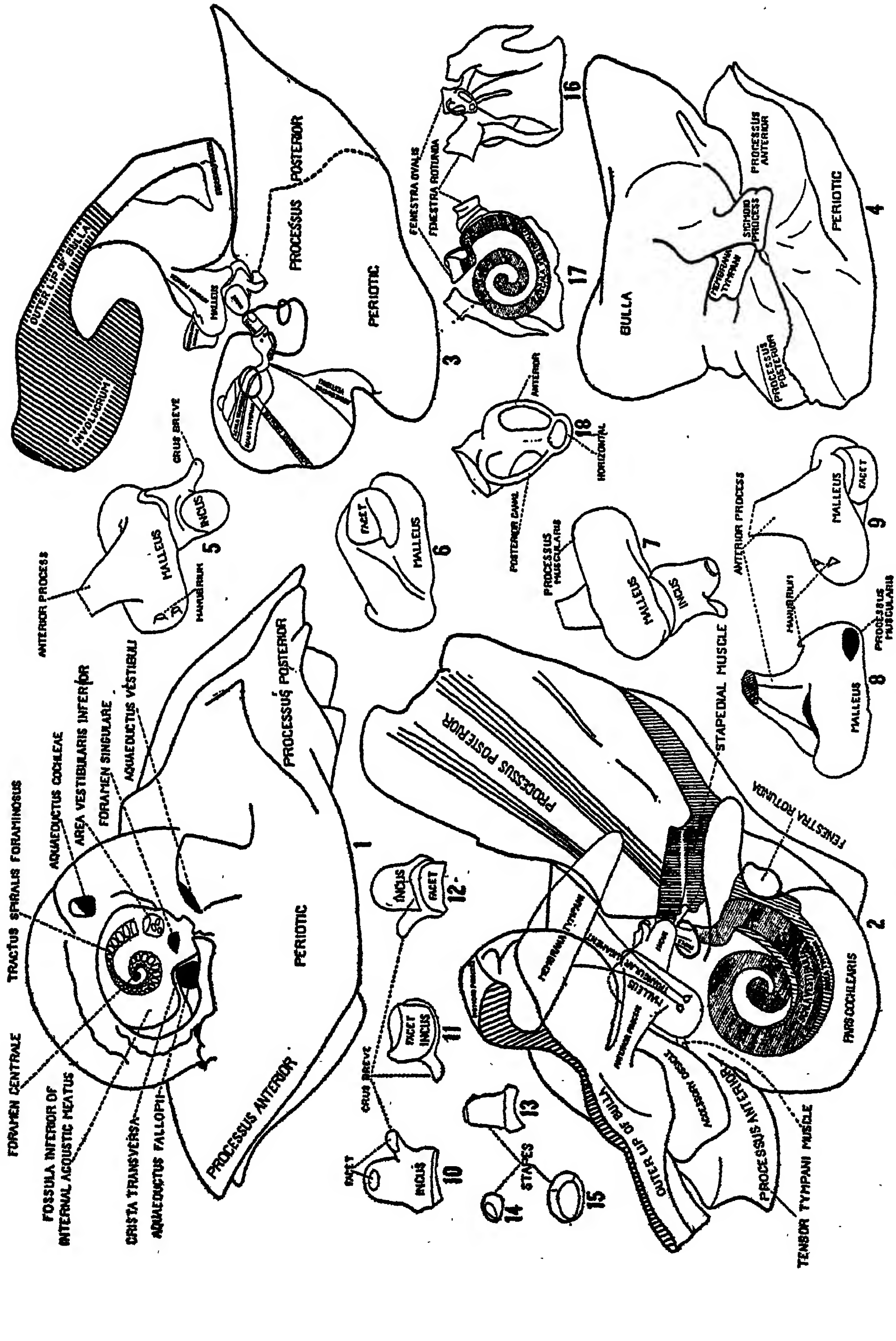


Fig. 23. Diagrams Illustrating Auditory Apparatus of Monodon monoceros

time the osseous portions of the inner ear have undergone certain changes, which brought about a diminishing utility for the tympanic membrane. We know that whales possessed at one time some sort of external ear, for a vestige of the auricular cartilage buried beneath the skin has been observed in some porpoises and the two outer ear muscles are still retained by baleen whales. The external auditory tube has been completely closed in the whalebone whales. This must have been accompanied by corresponding physiological adjustments to prevent the accumulation of an excess amount of wax in the blind tube. In many of the porpoises the outer orifice of the external auditory tube is so minute that one can not introduce the lead of a pencil, but the lumen expands in a trumpet-like manner as it approaches the ear drum. The tympanic bulla, periotic, malleus, incus, and stapes comprise the osseous portions of the organ of hearing; they lie outside the cranial cavity in a recess bounded by the squamosal, exoccipital, and basioccipital.

Whales have acquired an organ of hearing in which resonance must play an important part, for the malleus is rigid; the tensor tympani muscle, whose function in land mammals is to make taut the ear drum, is vestigial; and in some species the stapes is immovable in the vestibule. The tympanic bulla is the relatively dense and heavy sounding box fastened to the periotic by two thin pedicles, which can be set in vibration. Vibrations set up in these pedicles produce a corresponding amount of motion in the malleus, whose anterior process is likewise fused with the bulla between these pedicles, and it in turn transmits these vibrations to the incus and stapes. Another mechanical arrangement is thus acquired to take over the function ordinarily performed by the ear drum. Water-borne sound vibrations transmitted to the air contained in the tympanic bulla cause it to function as a sounding box, and its vibrations reach the cochlea by way of the ossicular chain and the vestibule. Dr. George L. Streeter at the request of the writer studied the brain of *Tursiops truncatus* and found that these porpoises have a highly developed central nervous system for the reception and disposal of cochlear stimuli, which stands out in contrast to the less well developed optic mechanism. The optic colliculus was found to be not more than one-fourth as large as the acoustic colliculus.

The organ of hearing as a whole and the soft structures associated with it appear to be especially well adapted for resisting temporary heavy pressure at considerable depths. The eustachian tube and lining membrane of the tympanic bulla communicate with several sinuses or reservoirs capable of distention with air. If these reservoirs are blown full of air and the lining membrane of the tympanic bulla distended before the animal dives, the external pressure exerted by the water on the tympanic membrane could be equalized by muscular compression of the associated air sinuses since the latter are all connected with the tympanic cavity.

A humpback whale (*Megaptera nodosa*) has an external auditory tube 21 inches in length. The outermost portion of this tube passes through the blubber and ends blindly about $5\frac{1}{2}$ inches from the external orifice, the tube itself decreasing in diameter from $\frac{1}{16}$ of an inch to almost nothing. Then comes an interval of 3 inches where the tube is completely closed. The innermost portion of the tube widens to a diameter of more than an inch and the walls are invariably collapsed. The tympanic membrane is in many respects the most remarkable structure

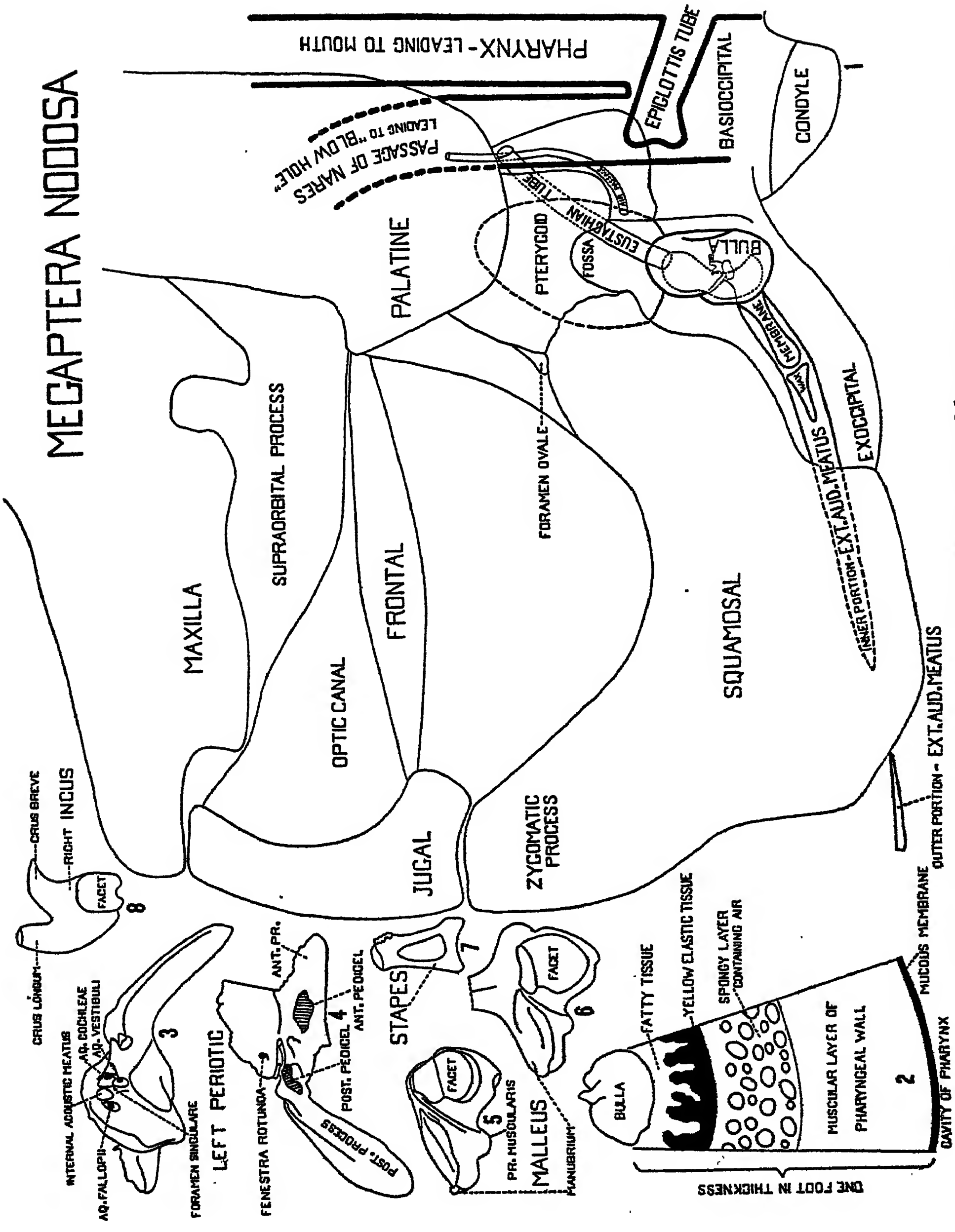


Fig. 24. Diagrams Illustrating Auditory Apparatus of Megaptera nodosa

connected with the organ of hearing. It is a finger-shaped structure, measuring about $3\frac{1}{2}$ inches in length, and is soft and flexible in a fresh state. Covering the bulla is a layer of elastic and fibrous tissue some three inches in thickness, which exudes fat, and this is covered by a 4 inch outer layer of spongy tissue with air spaces. To the latter is applied the muscular wall of the pharynx. Thus nearly a foot of tissue separates the tympanic bulla from the cavity of the pharynx. The periotic bones of living and fossil whalebone whales are all alike in that they have a long posterior process, which is wedged in between the exoccipital and squamosal bones.

Although the smaller porpoises are not accustomed to dive to such great depths as the whalebone whales, many of them have a partially calcified tympanic membrane. Yet in all these toothed whales the external orifice is so minute that it is practically closed. The rigid malleus articulates in the usual mammalian way with the incus, the long crus of the latter in turn with the head of the stapes, and the footplate of the stapes is sunk into the fenestra ovalis and arrested by the lining membrane of the vestibule. Notwithstanding these osteological obstacles, we do have evidence indicating that porpoises are irritated if not repelled by certain kinds of water-borne sounds. The conductive portions of the organ of hearing may be defective in certain respects, but the essential parts are retained. The cochlea is of the spiral type and varies from one and three-quarters to two full turns. In contrast to the whalebone whales, the porpoises, dolphins, sperm whales, beaked whales, and their relatives all have the ear bones attached to the skull by ligaments.

Zeuglodonts have been assumed to represent a part of the shallow water fauna of the Eocene period, and yet they have an organ for hearing of the type commonly associated with whales accustomed to diving to considerable depths. We have indisputable evidence that the tympanic bulla was in existence in this group of pelagic mammals at the beginning of the Middle Eocene age, for *Protocetus* has a bulla as fully developed as any living cetacean. Both the whalebone and the toothed whale types of periotic bones have been found associated with skulls of zeuglodonts. The cochlea is similar to those of living whales, and the anterior process of the malleus is fused with the bulla. It is thus apparent that some of these Eocene zeuglodonts had a rigid malleus and that the same limitations are placed upon the functioning of the organ of nearing as in most living cetaceans.

No matter how defective the cetacean organ of hearing may appear in comparison with those of land dwelling mammals, we have evidence that these modifications were present in some if not all of the earliest known zeuglodonts. If the conch-like bulla with its rigid malleus and pedicle method of attachment to the periotic arose in response to the requirements of an aquatic mode of life, these structures probably meet the exigencies of their environment, and are adapted for the perception of water-borne vibrations, for it is unlikely that so many diversified types of cetaceans would have survived until the present time if this organ were unsuited for their purposes.

LIST OF LITERATURE

Abel, O. 1905. Les Odontocètes du Boldérien (Miocène supérieur) d'Anvers. Mém. Mus. Roy. d'Hist. Nat. de Belgique, Bruxelles, vol. 3, pp. 1–155, text figs. 1–27.

———. 1913. Die Vorfahren der Bartenwale. Denkschr. k. Akad. Wiss. math.-nat. Kl., Wien, vol. 90, pp. 1–70, pls. 1–12.

———. 1924. Die Eroberungszüge der Wirbeltiere in die Meere der Vorzeit. Jena, pp. 121, text figs. 52.

Andrews, Roy C. 1914. The California gray whale (*Rhachianectes glaucus* Cope). Mem. Amer. Mus. Nat. Hist., New York, n. s., vol. 1, pt. 5, pp. 229–287, pls. 19–27, text figs. 22.

———. 1916. Whale Hunting with Gun and Camera. New York, pp. xxii + 333.

Augustin, W. 1913. Die Formvariabilität der Beckenknochen bei nordatlantischen Bartenwalen. Zool. Jahrb., Abth. f. Systematik, Jena, vol. 35, pp. 533–580, pls. 1–2.

Beddard, F. E. 1901. Contribution towards a knowledge of the osteology of the pigmy whale (*Neobalaena marginata*). Trans. Zool. Soc. London, vol. 16, pt. 2, pp. 87–110, pls. 7–9.

Brandt, J. F. 1873. Untersuchungen über die Fossilen und Subfossilen Cetaceen Europa's. Mém. Acad. Imp. Sci. de St.-Petersbourg (7), vol. 20, no. 1, pp. viii + 372, pls. 1–34.

——— 1874. Ergänzungen zu dem Fossilen Cetaceen Europa's. Mém. Acad. Imp. Sci. de St.-Petersbourg (7), vol. 21, no. 6, pp. iv + 54, pls. 1–5.

Cabrera, A. 1926. Cetaceos fosiles del Museo de La Plata. Revista del Museo de La Plata, Buenos Aires, vol. 29, pp. 363–411, text figs. 1–19.

Capellini, G. 1899. Balenottere mioceniche di San Michele presso Cagliari. Mem. Accad. Sci. Ist. di Bologna (5), vol. 7, pp. 269–287, pls. 1–2.

———. 1901. Balenottera Miocenica del Monte Titano, Repubblica di S. Marino. Mem. Accad. Sci. Ist. di Bologna (5), vol. 9, pp. 1–26, pls. 1–2.

———. 1902. Balene fossili Toscane. I. *Balaena etrusca*. Mem. Accad. Sci. Ist. di Bologna (5), vol. 9, pp. 1–22, pls. 1–3.

———. 1905. Balene fossili Toscane. III. *Idiocetus. Guicciardinii*. Mem. Accad. Sci. Ist. di Bologna (6), vol. 2, pp. 71–80, pls. 1–2.

Case, E. C. 1904. Cetacea. Miocene Text, pp. 1–56; Atlas, pls. 10–25. Maryland Geol. Survey, Baltimore.

Cope, E. D., 1895. Fourth contribution to the marine fauna of the Miocene period of the United States. Proc. Amer. Philos. Soc., Philadelphia, vol. 34, no. 147, pp. 135–154, pl. 6.

Dal Piaz, G. 1905. Sugli avanzi di *Cyrtodelphis sulcatus* dell' arenaria di Belluno. Pt. II. Palaeontographia Italica, Pisa, vol. 11, pp. 253–280, pls. 18–21, Text figs. 17–26.

Dart, R. A. 1923. The brain of the Zeuglodontidae (Cetacea). Proc. Zool. Soc. London, no. 42, pp. 615–648, text figs. 1–21.

Eschricht, D. F., and J. Reinhardt. 1866. On the Greenland right whale (*Balaena mysticetus* Linn.) with especial reference to its geographical distribution and migrations in times past and present, and to its external and internal characteristics. Ray Society, London, pp. 1–150, pls. 1–6, text figs.

Hanna, G. D., and M. E. McLellan. 1924. A new species of whale from the type locality of the Monterey Group. Proc. Calif. Acad. Sci., San Francisco, (4), vol. 13, pp. 237–241, pls. 5–9.

Kadic, O. 1907. *Mesocetus hungaricus* Kadic, eine neue Balaenopteridenart aus dem Miozän von Borbolya in Ungarn. Mitteil. Jahrb. Kgl. Ungarischen Geol. Anstalt, Budapest, vol. 16, pt. 2, pp. 21–91, pls. 3, text figs. 70.

Kellogg, R. 1922. Description of the skull of *Megaptera miocaena*, a fossil humpback whale from the Miocene diatomaceous earth of Lompoc, California. Proc. U. S. Nat. Mus., vol. 60, publ. 2435, pp. 1–18, pls. 4, text figs. 10.

———. 1924. Description of a new genus and species of whalebone whale from the Calvert cliffs, Maryland. Proc. U. S. Nat. Mus., vol. 63, publ. 2483, pp. 1–14, pls. 1–6.

———. 1924. A fossil porpoise from the Calvert formation of Maryland. Proc. U. S. Nat. Mus., vol. 63, publ. 2482, pp. 1–39, pls. 1–18.

———. 1925. Additions to the Tertiary history of the pelagic mammals on the Pacific Coast of North America. Publ. 348, Carnegie Institution of Washington, pp. 1–120, pls. 13.

———. 1926. Supplementary observations on the skull of the fossil porpoise *Zarhachis flagellator* Cope. Proc. U. S. Nat. Mus., vol. 67, publ. 2600, pp. 1–18, pls. 1–5.

———. 1927. Study of the skull of a fossil sperm whale from the Temblor Miocene of Southern California. Publ. 346, Carnegie Institution of Washington, pp. 1–24, pls. 1–9.

König, A. 1911. Ein neuer Fund von *Squalodon Ehrlichii* in den Linzer Sanden. Jahresb. Ver. Mus. Francisco-Carolinum, Linz, pp. 1–13, pl. 1.

Kükenthal, W. 1891. On the adaptation of mammals to aquatic life. Ann. & Mag. Nat. Hist., London (6), vol. 7, no. 38, pp. 153–179.

Leboucq, F. 1889. Recherches sur la morphologie de la main chez les Mammifères marins: Pinnipèdes, Siréniens, Cétacés. Archiv. de Biol., Liège, vol. 9, pp. 571–648, pls. 36–41.

Lillie, D. G. 1910. Observations on the anatomy and general biology of some members of the larger Cetacea. Proc. Zool. Soc. London, pp. 769–792, pl. 74, text figs. 69–78.

———. 1915. Cetacea. British Antarctic ("Terra Nova") Expedition, 1910. Natural History Report. Zoology, vol. 1, no. 3, pp. 85–124, pls. 1–8, text figs. 1–14. Publ. Brit. Mus. (Nat. Hist.), London.

Lydekker, R. 1894. Contributions to a knowledge of the fossil vertebrates of Argentina. Part II. Cetacean skulls from Patagonia. Annales del Museo de La Plata, vol. 2 for 1893, pp. 1–14, pls. 1–6, text figs. 2.

Matthiessen, L. 1886. Ueber den physikalisch-optischen Bau des Auges der Cetaceen und der Fische. Archiv ges. Physiol. Menschen u. Thiere, Bonn, vol. 38, pp. 521–528.

———. 1891. Die neueren Fortschritte in unserer Kenntnis von den optischen Baue des Auges der Wirbeltiere. Beiträge zur Psychologie und Physiologie der Sinnesorgane. Hermann von Helmholtz als Festgruss zu seinen siebsigsten Geburtstag. Hamburg und Leipzig, pp. 51–111.

———. 1893. Ueber den physikalisch-optischen Bau der Augen vom Knölwal (*Megaptera boops* Fabr.) und Finwal (*Balaenoptera musculus* Comp.). Zeitschrift für vergleichende Augenheilkunde, Wiesbaden, vol. 7, pp. 77–101, pls. 1–2.

Meyer, H. von. 1849. Neues Jahrbuch für Mineralogie, Stuttgart, p. 550; and *idem.*, 1850, p. 205.

Moreno, F. P. 1892. Lijeros apuntes sobre dos géneros de Cetáceos fósiles de la República Argentina. Revista del Museo de La Plata, vol. 3, pp. 393–400, pls. 10–11.

Neuville, H. 1921. Sur l'appareil respiratoire des Cétacés. Bull. Mus. Nat. d'hist. nat., Paris, Année 1921, no. 3, pp. 209–215, text figs. 1–2; *idem.*, no. 6, pp. 396–403, text figs. 1–2; *idem.*, Année 1922, no. 1, pp. 27–34, text fig. 1.

Pompeckj, J. F. 1922. Das Ohrskelett von *Zeuglodon* Senckenbergiana, Frankfurt a. M., vol. 4, pts. 3–4, pp. 43–100, pl. 2.

Portis, A. 1885. Catalogo descrittivo dei Talassoterii rinvenuti nei Terreni Terziarii del Piemonte e della Liguria. Mem. R. Accad. Sci. Torino (2) vol. 37, pp. 247–365, pls. 1–9.

Pütter, O. 1902. Die Augen der Wassersäugetiere. Zool. Jahrb., Abth. f. Anat. Jena, vol. 17, pp. 99–402, pls. 2–4, text figs. 45.

Ridewood, W. G. 1922. Observations on the skull in foetal specimens of whales of the genera *Megaptera* and *Balaenoptera*. Philos. Trans. Roy. Soc. London (B), vol. 211, pp. 209–272, text figs. 16.

Roux, W. 1883. Beiträge zur Morphologie der functionellen Anpassung. I. Structur eines hoch differenzirten bindegewebigen Organes (der Schwanzflosse des Delphin). Archiv. f. Anat. u. Physiol., Leipzig, pp. 76–162.

Stromer, E. 1908. Die Archaeoceti des Ägyptischen Eozäns. Beiträge z. Paläont. u. Geol. Österreich-Ungarns u. d. Orients, Wien, vol. 21, pp. 106–177, pls. 4–7.

Sudzuki, M. 1924. Untersuchungen über Cetacea. VIII, Über das Blut. Tôhoku Journ. Exper. Med. Sendai, vol. 5, nos. 4–5, pp. 419–427.

True, F. W. 1904. The whalebone whales of the North Atlantic, compared with those occurring in European waters, with some observations on the species of the North Pacific. Smithsonian Contrib. to Knowledge, vol. 33, no. 1414, pp. 1–331, pls. 1–50, text figs. 97.

———. 1912. The genera of fossil whalebone whales allied to *Balaenoptera*. Smithsonian Misc. Coll., vol. 59, publ. 2081, pp. 1–8.

Tullberg, T. 1883. Bau und Entwicklung der Barten bei *Balaenoptera sibbaldii*. Nova Acta Reg. soc. sci. Upsala (3), vol. 11, no. 8, pp. 1–36, pls. 1–7.

Van Beneden, P. J. 1875. La Baleine fossile du Musée de Milan. Bull. Acad. Roy. Sci. Belgique, Bruxelles (2), vol. 40, no. 12, pp. 736–758, pl. 1.

———. 1877–1886. Description des Ossements Fossiles des Environs d'Anvers. Pt. 2. Genres *Balænula*, *Balæna* et *Balænotus*. Ann. Mus. Roy. Hist. Nat. Belgique, sér. Paléont., Bruxelles, vol. 4, 1880, pp. 1–83, pls. 1–39. Pt. 3. Genres *Megaptera*, *Balaenoptera*, *Burtinopsis* et *Erpetocetus*. *Op. cit.*, vól. 7, 1882, pp. 1–90, pls. 40–109. Pt. 4. Genre *Plesiocetus*. *Op. cit.*, vol. 9, 1885, pp. 1–40. pls. 1–30. Pt. 5. Genres *Amphicetus*, *Heterocetus*, *Mesocetus*, *Idiocetus* et *Isocetus*. *Op. cit.*, vol. 13, 1886, pp. 1–139, pls. 1–75.

———. 1882. Une Baleine Fossile de Croatie, appartenant au genre Mésocète. Mém. Acad. Roy. Sci. Belgique, Bruxelles. vol. 45, no. 2, pp. 1–29, pls. 1–2.

Winge, H. 1921. A review of the interrelationships of the Cetacea. Smithsonian Misc. Coll., vol. 72, publ. 2650, pp. 1–97. [Translation by G. S. Miller, Jr., of Winge, H. 1918. Udsigt over Hvalernes indbyrdes Slaegtskab. Vidensk. Medd. fra Dansk. naturh. Foren., vol. 70, pp. 59–142.]

THE EFFECT OF CARBON DIOXIDE ON BACTERIA

By GEORGE VALLEY

Sterling Research Fellow, Laboratory of General Bacteriology, Yale University

IN 1848 Bethell patented a process for preserving milk by carbonation, which consisted in first boiling the milk to expel all the air contained in it and then saturating it with carbon dioxide. The milk, it was claimed, remained fresh for a long time after being exposed to the air. This process is more or less of prehistoric interest, since no evidence has survived to show how successful it was in its application.

DESTRUCTIVE EFFECTS OF CARBON DIOXIDE

Pasteur and Joubert (1877) observed that *B. anthracis* is killed in carbon dioxide. No mention is made of the media that were used in their experiment, nor is it stated how long the exposure to the gas continued, or how much carbon dioxide was required to react fatally to *B. anthracis*. Szpilman (1880) suggests that the above claim should be qualified somewhat, since he, Szpilman, showed definitely that from five to eight hours' exposure to an almost pure atmosphere of carbon dioxide did not kill *B. anthracis*, or even alter the pathogenicity. Grossmann and Mayerhausen report (1881) that CO_2 does not kill bacteria, but that it inhibits motility. Small amounts of CO_2 increased motility. Buchner (1885) has shown that the effect of carbon dioxide gas is variable. It inhibited Koch's Vibrio, but development was obtained with Fitch's Aethylbacillus, the Napel cholera bacillus and *Bact. typhosum*.

In 1885 and 1886 a series of papers by Pfuhl, Sohnke, Schaffer and Freudenreich, and Kolbe appeared. The investigations of Pfuhl and Sohnke dealt with the microörganisms found in carbonated waters. Schaffer and Freudenreich reported that typhoid and anthrax bacilli were unaffected in broth cultures under seven atmospheres of carbon dioxide pressure. Kolbe's work was an attempt to preserve meat and fruit in an atmosphere of carbon dioxide. Beef could be preserved for eighteen days, while mutton showed spoilage in a very short time.

Liborius (1886) failed in his attempts to initiate growth of *Cl. foetidum*, *Cl. polypiformis*, *Cl. oedematis-maligni* and *B. pseudo-oedematis* when carbon dioxide was passed through the medium. However, when it was passed over the surface of the medium some growth was obtained. Bolton (1886) reported a limited number of experiments with *M. aquatilis* and *B. erythosporus*. The results were erratic; inhibition was obtained in some cases but not in others. The duration of CO_2 treatment is not given. These experiments were carried out in water containing only traces of organic matter. Destruction of bacteria was also evident under hydrogen.

Leone's work appeared in a German translation in 1886, and concerned itself with the reduction of bacterial numbers in the city water of Munich. Reduction was obtained, but complete sterilization was never reported. The statement was made that pressure was not a factor in

these experiments, since carbon dioxide was applied at atmospheric pressure. The experiments as a whole offer only a very limited amount of data.

BACTERIA IN CARBONATED WATERS

Hochstetter's work (1887) was on the behavior of microörganisms in artificial carbonated waters, city water of Berlin and distilled water. This work has remained as a source of valuable information, and has probably not been surpassed in extent and comprehensiveness. The experiments included pure culture studies of *M. aurantiaca*, *E. prodigiosus*, pink yeast, a green fluorescent bacillus, a yellow bacillus, *M. tetragenus*, *Bact. lepisepticum*, *B. anthracis* (vegetative cells and spores), *Bact. typhosum*, alpha-bacillus, *V. cholerae*, spores of *Aspergillus flavescens*, and Finkler-Prior's bacillus. These organisms fell into three groups, according to their tolerance for carbon dioxide: (1) those which were viable for only a short time, (2) those which remained viable for a few weeks, and (3) those which survived for many weeks and even months.

According to Hochstetter's observations, there is no danger from cholera through carbonated waters, but the danger from typhoid fever is not altogether removed, since *Bact. typhosum* remains viable for from five to seven days. Epidemics of typhoid traced to carbonated waters occurred in Mainz in 1884. The author was able to control the development of bacteria in experimentally carbonated waters. Numerous organisms were found, however, in bottled beverages prepared under factory conditions.

Sirotinin (1888) reported a limited number of trials with *V. cholerae*, the Finkler-Prior spirillum, *Staph. albus*, *B. anthracis*, *B. cuniculicida* and *Bact. murisepticum*. There was complete inhibition of the last two organisms.

Fränkel (1889) reported a comprehensive series of experiments comprising forty different bacterial species. Gelatin medium was used in Esmarch tubes, and carbon dioxide gas was applied while the medium was still soft. It is noteworthy that inhibition or even killing was obtained with the organisms which are very sensitive to acid, for example *V. cholerae*. His observations were briefly summarized as follows: Certain common types of bacteria were able to develop in carbon dioxide as well as in the ordinary atmosphere; others were retarded, and a third group would not grow at room temperature, but would develop in CO_2 at higher incubation temperature. The effect of carbon dioxide was also tried on the saprophytic bacteria. The influence was not wholly inhibitive. The author believed that his results may be taken as a proof that carbon dioxide is a preservative or germicide. He stated at the same time that, in spite of this growth-inhibiting, or at times even killing, action, carbon dioxide should not be regarded as a sure means of preventing decomposition.

Weakening of pathogenic bacteria by CO_2 does not occur, according to him. The author also pointed out that in view of the unhindered growth of *Bact. typhosum* in a stream of CO_2, the so-called "harmlessness" of carbonated waters must be liberally interpreted.

Fränkel's work is similar to Hochstetter's in comprehensiveness, and, although conducted in a somewhat different manner, the conclusions arrived at are identical. Fränkel also observed that the reaction of the gelatin medium changed under the stream of carbon dioxide. He believed, however, that this change in reaction was inconsequen-

tial. It is, nevertheless, interesting to note that the acid-sensitive micro-organisms, such as *V. cholerae*, *B. anthracis*, etc., were most easily inhibited.

Frankland (1889) reported his experiments with *V. cholerae*, the Finkler-Prior vibrio and the organism of blue-green pus. His results are on the whole in accord with Fränkel's findings. He pointed out that certain differences in their results may be explained by variability in resistance of strains used. He confirmed Fränkel's observation that the majority of the organisms succumb readily. However, a small per cent remained alive and even multiplied to a certain extent.

Scala and Sanfelice (1891) investigated the effect of dissolved carbon dioxide in natural waters. It appeared that the pathogenic organisms, *V. cholerae*, *B. anthracis*, *Staph. aureus* and *albus*, *Bact. typhosum* and *Bact. lepisepticum* were not affected by the quantities of CO_2 naturally dissolved in water at 15°C. When the water was saturated with CO_2, *V. cholerae* and *B. anthracis* were injured, while others remained apparently indifferent. Carbon dioxide under pressure in soda-water was injurious to *B. subtilis*, while *Proteus vulgaris* remained unaffected. Spores of *B. subtilis* and *B. anthracis* did not germinate.

BACTERIA REQUIRING CARBON DIOXIDE

During the years 1890 to 1899 a very interesting observation was made and proven to be a fact, namely that though carbon dioxide exerts injurious effects on certain bacterial species, it is actually required by others. Vinogradsky (1890) and Vinogradsky and Omeliansky (1899) in a series of articles showed that the nitrifying organisms require carbon dioxide, utilizing it as a source of carbon. Godlewsky (1892) confirmed the original observation of Vinogradsky. These findings have been confirmed more recently by Meyerhof (1916–17) and Bonazzi (1921).

Considerable controversy developed between d'Arsonval and Charrin (1893) and Sabrazès and Bazin (1893). The former had recommended for the sterilization of organic filtrates an application of carbon dioxide under pressure of 50 to 60 atmospheres. They also reported, however, that *Ps. pyocyanea* cultures in broth were not killed under the given pressure of carbon dioxide during six hours' exposure. Sabrazès and Bazin repeated the work of d'Arsonval, but could not confirm his claims, even at higher pressures than those indicated by d'Arsonval, who suggested that certain organic liquids, such as blood, milk and urine, could be preserved in this manner. Sabrazès and Bazin experimented with *Staph. aureus*, *Bact. coli*, *B. anthracis* and *Bact. typhosum*, arriving at the conclusion that pressures of 90 atmospheres and beyond do not injure *B. anthracis* or *Staph. aureus*.

It would be of doubtful value to employ CO_2 for sterilization of organic liquids within the time limits fixed by d'Arsonval. In his reply to Sabrazès' criticism, d'Arsonval claimed that the differences in results were obviously due to differences in experimental technic. The sterilization in his experiments was effected with filtrates made up with glycerine to 15 or 20° Baumé. It was, therefore, the combined action of glycerin and of CO_2 under pressure which was responsible. He states very judiciously that "quant aux conditions de pression, de durée, de température, de composition chimique et de milieu nécessaires pour tuer les différents microbes pathogènes, c'est là une détermination pour laquelle je ne me suis pas senti une compétence suffisante."

Slater (1893) published a report on his examination of artificial carbonated waters sold and prepared under factory conditions. This was supplemented by some observations on water supplies used in their preparation and on experimentally prepared and inoculated carbonated waters. Slater used *Ps. fluorescens* liq., *Bact. coli-communis*, *Staph. aureus*, *Bact. typhosum*, *V. cholerae* and the Finkler-Prior spirillum. His experiments showed that, while killing or inhibition could be effected, it varied with the organism in question. The destructive action was intensified in storage, being most noticeable after three weeks, but not necessarily of a constant occurrence. He observed that artificial carbonated waters are by no means sterile, although the numbers of bacteria present are not an index of the original purity of water used in the preparation.

Haenle's work (1905) supplements that of Slater. He made further observations on the necessity of cleanliness and sanitary conditions of bottling plants. Natural mineral waters are normally almost sterile or completely sterile when issuing from the ground. Differences were observed with different kinds of bottles, i.e., siphons, corked, or capped bottles. The siphons were apparently the most sanitary. When a sample contained more than 300 organisms per cubic centimeter it was considered by him as having been stored in dirty bottles.

A series of articles which appeared in 1895 to 1899 by Czaplewsky, Draer, and Morgenroth could not be obtained in the original. It appears, however, from available abstracts that these reports were in perfect accord with those mentioned here, and in general emphasize the necessity of more or less prolonged storage of carbonated waters intended for human consumption.

STIMULATING ACTION ON PIGMENTATION

Lubinski (1894) and Neumann (1897) observed that pigment-producing organisms such as *Staph. aureus* are devoid of color under anaerobic conditions, but develop abundant pigmentation when reëxposed to air. The cultures which were grown in carbon dioxide and had lost their color had the pigmentation restored much more rapidly than those which were subjected to hydrogen. Consequently, the conclusion is drawn that carbon dioxide exercises a certain stimulating action on pigmentation.

The present writer's experience has shown that this observation holds true also with *E. prodigiosus*. In an atmosphere enriched with 1 per cent carbon dioxide very intense pigmentation bordering on a dark maroon was obtained. By reducing the carbon dioxide content below that which is normally found in the air only a very slight color was obtained, that is, a faint shade of pink.

Hoffmann's work (1906) comprised a series of experiments with carbon dioxide on the colon-typhoid group in water, nutrient broth and milk. High pressures of carbon dioxide were used. This author realized that a very small number of bacteria may persist in the medium after the treatment with CO_2; hence he used an enrichment cultivation method. By adding 1 per cent peptone broth to the liquid after the carbonation, and incubating the whole quantity, he was able to obtain subsequent growth on plates and in broth, whereas he failed to detect viable organisms by the usual inoculation transfer method. Sterilization in water suspension was obtained at 50 atmospheres of carbon dioxide in from 2 to 3 hours with *Bact. coli* and the dysentery bacillus. Minute traces of organic matter or other nutrient material when present tended to render the results irregular.

EFFECT ON BACTERIA IN MILK

Hoffmann's experiments with milk were unique. No other work of a similar nature has come under the writer's observation. This author investigated the effect of carbon dioxide on the bacteria in milk, and on the milk itself. Under 50 atmospheres of carbon dioxide the bacterial count could be materially reduced in 48 hours, (from 1,012,930 at the start to 7,276); but complete sterilization was evidently never obtained. The results were no better when the milk was heated to 50°C for 20 minutes. The reduction was more marked, but a slow curdling of milk took place. The observation was made that carbon dioxide exerts considerable influence on sterile milk. After allowing 50 atmospheres of carbon dioxide to act at 56° for 24 hours on raw milk, the casein could easily be separated from the whey. It was observed that samples of raw milk under 10 atmospheres of carbon dioxide pressure remained in apparently good condition for at least 72 hours. The untreated samples curdled in 24 hours. The author concluded that the question of milk sterilization by CO_2 was far from satisfactory.

Altana (1907) experimented with 75 different organisms, including higher bacteria, moulds and yeasts, and according to his results divided the organisms studied into three different groups as follows: (a) those which were completely inhibited by carbon dioxide (high tension), (2) those that were not affected at all by this agent, and (3) an intermediate group composed of species that were more or less variable.

Van Slyke and Bosworth (1907) investigated the preserving action of CO_2 on milk. Lactic fermentation was delayed in CO_2 under pressure. No noticeable effect was observed under ordinary atmospheric pressure, however.

Berghaus (1907) subjected thirteen species of microörganisms to various pressures, under carbon dioxide. His list comprised the following: *V. cholerae*, *B. anthracis*, *Bact. typhosum*, *Bact. coli*, *Bact. fecalis-alkaligenes*, *Bact. enteritidis* Gaertner, *Bact. dysenteriae* (Shiga-Kruse and Flexner), *Bact. paratyphosum* A and B, *Staph. aureus*, *Ps. pyocyanea* and *Proteus vulgaris*. These organisms were subjected to carbon dioxide on freshly poured agar plates for a period of 24 hours, at 37°C. The strains under investigation were divided into three groups as follows: (1) *V. cholerae* (killed in 24 hours at one atmosphere pressure), (2) *B. anthracis* and *Bact. fecalis-alkaligenes* (growth inhibited in 24 hours, but no killing), and (3) *Bact. coli* and *Bact. enteritidis* (able to develop under two atmospheres of carbon dioxide pressure). Variations in resistance were shown by various strains of *Bact. coli*. Four of the strains required 15 atmospheres of carbon dioxide, while with two other strains a pressure of 9 atmospheres was sufficient to kill.

During the period from 1911 to 1915 a series of articles by the following investigators appeared, dealing with various phases of bacteriology in carbonated beverages: Klein (1911), Young and Sherwood (1911), Eldson (1912), Allen, LaBach, Pinnell and Brown (1915) and Colin (1915). Aside from variations in experimental technic, different organisms studied, and the objects or aims which prompted the investigations, certain observations are common to all of these works. According to them, carbonated beverages found on the market may or may not be free from living microörganisms. Reduction could be obtained with the pathogenic forms, but not complete sterilization. The sources of microörganisms in commercial products are evidently unclean bottles and unsanitary conditions

of the plant. The work of Allen, LaBach, Pinnell and Brown is particularly illuminating.

Colin's (1915) experiments were conducted with sterile water, into which broth cultures of the test organisms were introduced. Pressures varying from 10 to 24 kilos were then applied for varying lengths of time, generally from one to twelve hours. *Bact. typhosum*, *Bact. coli*, *Bact. dysenteriae* (Shiga), *V. cholerae*, *Ps. pyocyanea*, *C. diphtheriae* and *B. subtilis* were subjected to study under carbon dioxide pressures. Sterilization was effected with *Bact. typhosum* in 20 hours or more at 10 kilograms CO_2 pressure. With *C. diphtheriae* sterilization was obtained at 10, 15, and 20 atmospheres after 24, 9, and 3 hours respectively. *Bact. coli* persisted for 5 days under 25 kilo pressure.

In 1911 another departure from the study of the destructive effects of carbon dioxide on bacteria occurred. Lieske reported that *Spirophyllum ferrugineum* is benefited by the presence of carbon dioxide. The growth of the organism was considerably increased by this gas, and inhibited by the presence of organic matter.

Wherry and Oliver (1916), following Nowak's work of 1908, grew the gonococcus and several other organisms under reduced oxygen tension. It was emphasized that some parasitic species could be isolated or made to grow considerably better under partial tension than under full anaerobic or aerobic conditions. No mention is made of carbon dioxide influence. Five bacterial species in all were used, including *Bact. typhosum*.

Cohen and Markle (1916) reported a successful primary isolation of meningococcus under partial oxygen tension, but no mention is made of any possible influence of carbon dioxide as such.

Wherry and Ervin (1918) furnished some experimental data which indicated that carbon dioxide is necessary for the growth of *M. tuberculosis*. Saprophytic and non-saprophytic strains were used in the experiments, and were found to be alike in their failure to grow in the absence of carbon dioxide.

Larsen, Hartzell and Diehl (1918), in an effort to produce antigenic material in a diffused state, resorted to high pressures under various gases. Carbon dioxide was fatal to *Bact. typhosum*, *Bact. coli*, *M. tuberculosis*, *Ps. pyocyanea*, staphylococci, streptococci and pneumococci in from 1.5 to 2.5 hours. Pressures of carbon dioxide under 40 atmospheres did not produce any visible effect on the bacteria studied. The action of this gas under pressure was more destructive in distilled water than in nutrient broth. Yeast cells resisted it much longer than 24 hours.

BENEFICIAL EFFECT OF CARBON DIOXIDE

Cohen and Fleming (1918) made use of the tandem cultivation method in their meningococcus studies; they also supplied carbon dioxide gas as such, in amounts varying from 10 to 75 per cent. Their results showed that as good growth could be obtained by supplying the gaseous CO_2 as with the *B. subtilis* culture method. The optimum concentration varied from 10 to 30 per cent carbon dioxide. With from 50 to 75 per cent of the gas the growth was scant. Their explanation was that the CO_2 dilutes the oxygen and thereby helps the growth; i.e., the partial tension phase was strongly emphasized.

In the same year (1918) MacKenzie reported that 22 per cent carbon dioxide was bactericidal for the meningococcus in Ringer-Locke solution, in 20 minutes. Ruediger (1919) confirmed the partial tension idea by obtaining good growth of the meningococcus in stoppered tubes. There was no growth when the tubes were

left open. It may be presumed that the CO_2 liberated during respiration diluted the oxygen.

Chapin (1918), following Wherry's technique in primary isolation of the gonococcus, carried the method a point further, and applied carbon dioxide gas directly. He obtained good growth over a wide variety of concentrations. The author also suggested that the growth of *B. subtilis* not only diminishes oxygen, but supplies carbon dioxide as well. Hence, the same object could be attained by supplying CO_2 or by placing a lighted candle in the jar with the plates.

Cohen's work was severely criticized by Gates (1919). The latter claimed that ascribing microaerophilic properties to the meningococcus was an error, since the organisms would grow successfully in atmospheres of 24, 32 and 40 per cent oxygen. Reduction of oxygen to 15 and 18 per cent respectively showed no inhibitive or benefitting influence over the control plates kept under ordinary atmospheric conditions. Growths were equally good at any points within 10 and 30 per cent carbon dioxide, as long as the reaction of the medium remained favorable. The author concluded that if there was any effect from carbon dioxide it was due to changing the reaction of the medium and making it favorable for the meningococcus.

St. John (1919) denied that there is any influence exerted by CO_2 on the meningococcus, and attributed the beneficial results entirely to the increased moisture content in the closed system. Kohman (1919) supported the view that carbon dioxide is beneficial to the meningococcus, by delicately adjusting the reaction to the optimum pH range of the meningococcus. By this adjustment a buffer system was created and further deviations of pH prevented.

Stokes (1920), and Gershenfeld (1920) published their results of examinations of carbonated beverages, undertaken largely from the public health standpoint. It appears, according to them, that a very large per cent of carbonated beverages on the market showed high bacterial counts. The possibility of intestinal infection through the consumption of such beverages is pointed out.

The interest in primary cultivation of the gonococcus and other organisms of this type under increased carbon dioxide tension, or sometimes reduced oxygen tension, has not in the least abated. Herrold (1920) described a modification of the partial tension method whereby good results were obtained. This consisted in inverting the plates inoculated with gonorrheal material over a plate inoculated with *B. subtilis*, and joining the two plates with a rubber band. Bicarbonate was used also, instead of *B. subtilis* in the lower plate. By the addition of 1 per cent sulphuric acid carbon dioxide was liberated and the conditions necessary for growth furnished.

Swartz and Davis (1920) created partial tension conditions by heating the tubes and sealing them with rubber stoppers. Upon cooling, reduced tension was obtained. This facilitated the handling of a large number of cultures.

Huddleson (1920) changed from the *B. subtilis* tandem culture method for culturing *Bact. abortus* to one in which an atmosphere containing 10 per cent carbon dioxide by volume was employed. The same object, i.e., increased CO_2 content, was attained by him when the culture tubes were sealed. His observations are in accord with those of Cohen and Fleming (1918), and of Ruediger (1919), with the meningococcus, and of Chapin (1918) with the gonococcus. He apparently recognized the importance of carbon dioxide

as such in the cultivation of *Bact. abortus*, rather than the necessity of reduced oxygen.

ADAPTATION OF BACTERIA TO DIFFERENT GASES

Rockwell and McKann (1921) investigated the effects of various gaseous environments on the growth of the gonococcus. Their results showed that this organism could be trained to tolerate rather high concentrations of hydrogen, carbon dioxide and oxygen, when mixed with air or in combination with each other. When a certain strain had become adapted to grow under high concentration of hydrogen, growth was inhibited by the presence of much oxygen and carbon dioxide. As high as 100 per cent of any one of these gases could be used in growing the organism. They concluded, therefore, that the gonococcus can be made to grow under various gaseous environments. It is believed by them that such expressions as aerobic, anaerobic or partial-tension strains, are expressions of the previous gaseous adaptations in nature.

Rockwell (1921) studied the gaseous requirements of the gonococcus, *B. subtilis*, *M. tuberculosis* 801, 802, and 803, *Bact. coli*, *Staph. aureus*, *Prot. vulgaris*, and *B. anthracis; Cl. welchii* and *Cl. tetani* were the anaerobes used. Enclosing the cultures either in hydrogen or nitrogen, or under anaerobic conditions with pyrogallol, it was observed that the cultures failed to grow. If, however, the respiratory CO_2 was not removed, or if CO_2 was supplied to cultures under nitrogen, growth followed. The author concluded that growth of the aerobic bacteria and those of the facultative group is in some way favored by CO_2.

Torrey and Buckell (1921) refuted the idea of a reduced oxygen requirement for the gonococcus, and believed that success in obtaining growth in a closed system is due entirely to the increased moisture retained in the medium or in the air over the medium.

Corper, Gauss and Reusch (1921) reported inhibition of *M. tuberculosis* without carbon dioxide, and inhibition of growth when the CO_2 approached 3 per cent; they considered 12 per cent CO_2 definitely tuberculocidal. In further studies concerning the importance of the growth of tubercle bacilli as determined by gaseous tension Corper, Lurie and Uyei (1927) conclude that a slightly better growth is observed in an atmosphere enriched with carbon dioxide than without the added CO_2.

COLON-TYPHOID BACTERIA IN CARBONATED WATERS

Koser and Skinner (1922) investigated the viability of the colon-typhoid group of organisms in carbonated waters and carbonated beverages. In their experiments the waters and beverages under observation were prepared under experimental conditions simulating those of the factory as far as possible. The authors came to the conclusion that the chief bactericidal influence of CO_2 was due to the increased hydrogen ion concentration in the solution. *Bact. coli* showed considerable resistance to carbon dioxide and could be recovered from various non-acid beverages after 7 days under 28 lbs. pressure at 24°C. In acid beverages the longevity of *Bact. coli* was reduced. The plates were sterile in 3 days, but not in 24 hours. When kept at 1°C, viable organisms were not recovered in 10 cc. amounts of the liquids after one month. *Bact. typhosum* was less resistant. It was evidently destroyed in 24 hours at 25 pounds pressure, at room temperature. At 1°C, this organism persisted for 4 days. Paratyphosum B. was positive in 10 cc.

after 48 hours at 23 pounds pressure and 24°C. At 1°C. the same organism was found to be alive in 10 cc. after 10 days. The spores of *B. mesentericus* and *B. subtilis* were found to persist in carbonated water in their original numbers after one month.

Prucha, Brannon and Ambrose (1922) investigated the effect of carbon dioxide on bacteria in milk and ice cream. It was found that there was no destruction of bacteria when the milk containing *Bact. coli* and *Bact. typhosum* was subjected to from 10 to 30 pounds extra pressure, under carbon dioxide. Under 20 pounds pressure there was an increase from 47,000,000 to 153,000,000 per cc. of milk. They also showed that there was no decrease of bacteria in ice cream, due to carbon dioxide. Even after six months in storage the carbonated ice cream had as many bacteria per cc. as the plain ice cream.

Erickson and Albert (1922) reported their experiments with various methods of producing reduced oxygen-tension for the gonococcus, and came to the conclusion that the beneficial effects are entirely due to an increased amount of moisture. Fitch (1922), when using Huddleson's method for enriching the atmosphere with CO_2, found difficulty from liberated chlorine. He grew duplicate sets of cultures, one in carbon dioxide and the other set in hydrogen, and evidently found no difference in favor of carbon dioxide. He concluded that Huddleson's claim for a specific action of CO_2 is not proven, and that this gas probably does nothing more than to dilute the oxygen.

Lorentz (1923) observed that the diphtheria organism, when grown under CO_2, became longer and more slender. The granules were increased in size and thickened. The number of positive diphtheria cases was found to be 30 per cent higher when the field cultures were grown under added CO_2, instead of ordinary air.

Rockwell (1923) reported additional work on gaseous environmental studies, on ten different organisms. The list comprises *B. subtilis*, *M. tuberculosis* (saprophytic strain), *Prot. vulgaris*, *Staph. aureus*, *Cl. welchii*, an anaerobe from hide, pneumococcus pus, streptococcus pus, and the meningococcus. Throughout the experiment, conducted under aerobic conditions, with nitrogen gas, nitrogen and carbon dioxide, and under conditions of anaerobiosis with pyrogallol and partial tension, growth was obtained under nitrogen and carbon dioxide with all of the various organisms used. Further division of partial-tension organisms was made by him according to their tolerance for oxygen.

Donald, Jones and MacLeon (1924) reported experimental work on artificially inoculated beverages. *Bact. coli* and *Bact. typhosum* were used as the test organisms. A study of the curves shows a very interesting relationship between high pressure and storage. The decline in bacterial numbers seems directly proportional to both. With a pressure of 95 pounds the beverages were apparently sterile after 5 days at room temperature. The curve shows that with 15 pounds bottling pressure there was a decline, but after 6 weeks the curve is still above the zero line. At 37.5°C. the bactericidal effect of CO_2 caused sterilization in one week. In general, it is apparent that after 34 days at 20°C., and at 37.5°C., the beverages showed bacteria present under all conditions and pressures of the experiment. The pressures were 70 and 45 pounds respectively. A second series of beverages was prepared and inoculated very lightly. *Bact. typhosum* did not show any rise in numbers under high pressure (70 pounds).

Bact. coli gave an increased count under 45 and 70 pounds extra CO_2 pressure up to ten days. *Bact. typhosum* increased in numbers under low (45 pounds) pressure. Complete sterility was evidently not reached within 30 days, when 20 organisms per cc. were inoculated into ginger ale.

Hunziker (1924) reported his experiments concerning the effect of carbon dioxide on butter. Two lots of butter were churned experimentally on a commercial scale. One-half of the cream was given carbon dioxide treatment. No bacterial counts are given, but the examination showed that the carbonated butter had turned rancid, and the score dropped from 89 points (fresh butter) to 83 points at the end of 12 weeks. This would indicate that carbonation cannot be relied upon to prevent bacterial deterioration of butter.

Prucha, Brannon and Ruehe (1925) concluded that if any appreciable benefit is to be expected from the carbonation of butter, it is necessary to store the butter in an atmosphere of CO_2 in an air tight container.

EFFECT ON BACTERIUM ABORTUS

Theobald Smith (1924) reported studies with *Bact. abortus*, which had extended over a period of two years. It is noteworthy to observe that freshly isolated strains yielded better growth under CO_2 than under ordinary atmosphere. According to him, certain strains may not develop at all in the open culture tube. It was found, further, that by removing the CO_2 with sodium hydrate, growth is inhibited completely in freshly isolated strains, and materially retarded in old strains. It developed further that as high as 100 per cent carbon dioxide could be tolerated by the organism. There was, however, some retardation of growth. Growth of certain strains appeared in eleven day old tubes, under carbon dioxide, which had shown no indications of development under ordinary atmospheric conditions. The author suggests that further studies may show that *Bact. abortus* (Bang) is the only pathogenic organism which possesses such a CO_2 relationship. It is further pointed out that the different strains of *Bact. abortus* fall into two groups, parasitic and saprophytic. In a later work (1926) the same writer stated that this relationship to CO_2 may serve a useful purpose in differentiating *Bact. abortus* strains into the bovine type on the one hand, and the so-called vaccinal or persistent udder strains on the other.

Rockwell (1924) advocated the use of carbon dioxide in anaerobic cultures, and presented experimental evidence of successful cultural work by this method, with *Cl. welchii*, *Cl. tetani*, an organism from chronic bronchitis, and with *Cl. botulinum*.

Sierakowski and Zajdel (1924), discussing the rôle of carbon dioxide in hermetically sealed bacterial cultures, observed that this gas adjusts the final H-ion concentration to pH 6.8. This they claimed to be true in all bacterial cultures. Evidence to this effect was offered for *B. dysenteriae* (Flexner), *Bact. typhosum*, *Bact. paratyphosum* A, B, and C, *Bact. coli*, *V. cholerae*, *C. diphtheriae*, *Prot. vulgaris* and *Staphylococcus*. Five day old cultures, when stoppered, do not acidify, that is reach a pH of 6.8, since these are evidently dying off and do not produce CO_2. According to them, production of CO_2 may be taken as an indication of viability in a culture.

Novy and Soule (1925) arrived at the conclusion that *M. tuberculosis* does not require CO_2 for its development, and that it is not inhibited, therefore, by the removal of carbon dioxide from the cul-

ture. Whatever inhibition has been observed by earlier workers and by Novy and Soule under certain conditions was, according to them, entirely due to desiccation. This conclusion was challenged, however, by Rockwell and Highberger (1926), who confirm Wherry's former findings that *M. tuberculosis* cannot develop without carbon dioxide and that the inhibitive effect is not due to desiccation. It was shown that with as much as 40 per cent dehydration (by sulphuric acid) growth was as good as in the control tube.

In the realm of autotrophic bacteria, Waksman and Starkey (1922–23) and Starkey (1925) have shown that the sulphur oxidizing bacillus, *Thiobacillus thiooxidans*, requires and utilizes carbon dioxide in a manner similar to the nitrifying organisms.

Masur (1926) reported that he was able to cultivate a strain of tubercle bacillus for sixteen generations in a medium containing no carbon except the carbon dioxide of the air. An experiment was also described which indicates that this organism will not develop in the absence of free carbonic acid gas. The investigator concludes that "under certain conditions the tubercle bacillus can utilize directly the carbon dioxide of the atmosphere."

Kulp (1926) based his method of determining the viability of *L. acidophilus* on the principle recently announced by Valley and Rettger (*vide infra*) that carbon dioxide is necessary for bacterial development. Carbonic acid gas, ten per cent by volume, is supplied to the agar plates in a special closed container. Considerably higher viability counts are obtained in this manner than by the customary open method. Furthermore, the colonies are also larger and, as a rule, more characteristic.

INHIBITION OF BACTERIAL GROWTH IN ABSENCE OF CARBON DIOXIDE

Valley and Rettger (1925, 1926, 1927) studied a large number of bacterial species and individual strains and their response (1) to high concentrations of carbon dioxide, and (2) to complete carbon dioxide removal from the environment. From their studies it is evident that the inhibiting effects observed with high concentrations of carbon dioxide (30 to 100 per cent) are primarily, and in many instances entirely, due to increased H-ion concentration of the medium. Displacement of oxygen from the environment by the large amounts of CO_2 gas is often a factor also. They have found, on the other hand, that bacterial growth is inhibited by the complete removal of carbon dioxide from the cultural environment. Under carbon dioxide-free, but otherwise favorable conditions, many of the organisms employed were actually killed in 24 to 48 hours, presumably as the result of complete inanition. A total of 109 different organisms were studied, the selection comprising several important representatives of the various bacterial groups. These authors found that the minimum CO_2 requirement for the various groups or species varied within wide limits.

The findings of Valley and Rettger were corroborated by Rockwell and Highberger (1927), who reported that *Bact. coli*, *Pr. vulgaris* (*B. proteus*), *Ps. pyocyanea* and *Staph. albus* were inhibited in their growth by the removal of carbon dioxide from the environment. The latter investigators also showed that a strain of yeast (*Saccharomyces*) and a strain of mold (*Mucor*) were likewise inhibited by the removal of carbon dioxide.

Rippel and Bortels (1927) have shown that *Aspergillus niger* spores germinate very poorly when cultivated under CO_2-

free conditions. This recent observation is in full accord with that of Durrell (1924), namely that the spores of *Basisporum gallarum* do not germinate in the absence of carbon dioxide, and are in turn stimulated by small amounts of added CO_2 gas.

Phelon, Duthie and McLeod (1927) attempted to employ oxygen-carbon dioxide mixture for the aeration of meningococcus cultures. Their object was to prevent extreme alkalization of the culture. With a gas mixture containing 20 per cent carbon dioxide it was possible to maintain the culture fluid at pH 7.0 and to prolong the life of the culture slightly beyond that of the control, which was aerated with an oxygen nitrogen mixture.

Plastridge and Rettger (1927) have employed gaseous carbon dioxide for aeration purposes in experimental diphtheria toxin production. In cultures which were grown in an atmosphere enriched with 3 per cent carbon dioxide highly potent toxin was produced with regularity. Deterioration of the toxin was prevented in the original culture, even during several weeks of continued incubation. These authors have since found that the filtered toxin is stable under CO_2 at various temperatures of storage. It was further observed that the culture of *C. diphtheriae* under increased carbon dioxide tension contained many more viable organisms than those grown under the usual conditions. The initial H-ion concentration was fairly evenly maintained during the incubation, by passing a slow stream of ordinary air containing from 3 to 5 per cent of added carbon dioxide over the culture.

CONCLUSIONS

In this review, the investigations dealing more or less with the effects of carbon dioxide on bacteria are given in chronological sequence. According to subject matter, they could be grouped as follows:

(1) Those that were concerned with the destructive action of CO_2 on bacteria, pro and con. The period covered here extends approximately from 1877 to 1915, though some work on this phase has appeared as late as 1924, or even later.

(2) Those investigations which deal with the beneficial influence of carbon dioxide, also pro and con. The beginning of this second period was probably signalled by Nowak's partial-tension method for the cultivation of *Bact. abortus* (Bang) in 1908, but more definitely in 1916, with Wherry and Oliver's contribution to the study of the gonococcus, although still under the conception of the partial tension idea. Chapin (1918) applied gaseous CO_2 in the cultivation of the gonococcus, and Cohen and Fleming employed this gas in the primary cultivation of the meningococcus.

(3) Studies concerned with carbon dioxide as a definite requirement. The conception that CO_2 may be necessary or absolutely essential to bacterial growth has been very gradual in its development. Vinogradsky (1890) proved that CO_2 is necessary for the nitrifying bacteria. Lieske (1911) found the same to be true for *Spirophyllum ferrugineum*. Wherry and Ervin (1918) were the first apparently to recognize this requirement for the tubercle bacillus, and their observations were later confirmed by Rockwell and Highberger. Theobald Smith (1924) observed that CO_2 is necessary for *Bact. abortus*, since the organism failed to grow in the presence of sodium hydrate. Valley and Rettger (1925, 1926, 1927) reported that complete inhibition of growth of common laboratory stock cultures had been obtained by CO_2 exclusion, and that CO_2 is necessary for bacterial development.

It will be seen from the above review that experimental evidence concerning the effect of carbon dioxide on bacteria has been accumulating during the past fifty years. The efforts of the earlier workers were for the most part directed to a study of the inhibitive action of carbon dioxide on bacterial growth.

Gradually another line of evidence has been accumulating. It has become more and more apparent that this agent, though it exerts a harmful influence on bacteria under certain conditions, may be of supreme importance, whether directly or indirectly, in their economy. The application of added carbon dioxide gas in the primary cultivation of the so-called partial tension organisms (*Bact. abortus* and *L. acidophilus*, for example) furnishes ample evidence to support this view.

Finally, observations of the past five or six years have brought forward the conception that carbon dioxide as such is necessary for bacterial growth and development, and therefore, for life itself. This conception rests on experimental evidence obtained with various bacterial species, particularly by Valley and Rettger, who found that of 109 different organisms employed in their carbon dioxide studies none could be made to develop in otherwise favorable culture media when they were deprived of all carbon dioxide.

The author desires to express his thanks to Professor Leo F. Rettger of Yale University for many valuable suggestions and for critical reading of the manuscript.

LIST OF LITERATURE

Allen, R. M., LaBach, J. C., Pinnell, W. P., and Brown, L. A. 1915. Non-alcoholic carbonated beverages, sanitary condition and composition. Kentucky Agr. Exp. Sta. Bull. 192.

Altana, Giuseppe. 1907. Sull'azione tossica dell'anidride carbonica sui microrganismi. Riv. d'ig. e di san. Pubbl., 16 mai, 293–308.

d'Arsonval. 1893. Remarques à propos des notes de MM. Sabrazès et Bazin. Compt. rend. Soc. Biol., *5*, 914–916.

d'Arsonval et Charrin. 1893. Pression et microbes. Compt. rend. Soc. Biol., *5*, 532.

Beijerinck, M. W. 1904. Ueber die Bakterien, welche sich im Dunkeln mit Kohlensäure als Kohlenstoff-quelle ernähren können. Centr. Bakt. Parasitenk., Abt. II, *2*, 593–599.

Berghaus. 1907. Ueber die Wirkung der Kohlensäure, des Sauerstoffs und Wasserstoffs auf Bakterien bei verschiedenen Druckhöhen. Arch. f. Hyg., *62*, 172–194. (172–199).

Bolton, Meade. 1886. Ueber das Verhalten verschiedener Bakterien im Trinkwasser. Z. f. Hyg., *1*, (76–114) See p. 100.

Bonazzi, Augusto. 1921. On nitrification. J. Bact., *6*, 479–499.

Bruschettini, A. 1907. A proposito dell'azione tossica dell'anidride carbonica sui microrganismi. Riv. d'ig. e di san. Pubbl., 16 juin, *18*, 365–366.

Buchner, Hans. 1885. Beiträge zur Kenntnis der Neapeler Cholera Bacillus und einiger demselben nahestehender Spaltpilze. Arch. f. Hyg., *3*, 411–414.

Chapin. C. W. 1918. Carbon dioxide in the primary cultivation of the gonococcus. J. Inf. Dis., *23*, 342–343.

Cohen, M. B., and Markle, Louis. 1916. A method which greatly facilitates the cultivation of the meningococcus. J. Am. Med. Assoc., *67*, 1302–1303.

Cohen, M. B., and Fleming, J. S. 1918. The diagnosis of epidemic meningitis and the control of its treatment by rapid bacteriologic and serologic methods. J. Inf. Dis., *23*, 337–341.

Colin, H. 1915. Sterilisation de l'eau par l'acide carbonique sous pression. Compt. rend. Ac. Sci., *161*, 652–655.

Collingridge-Klein. 1911. Soda-Water. Analyst, *36*, 16.

Corper, H. J., Gauss, H., and Rensch, O. B., 1921. Studies on the influence of carbon dioxide on resistance to tuberculosis. Am. Rev. Tuberculosis, 5, no. 7, 562–587; *also* J. Am. Med. Assoc., *76*, 1216–1218.

Corper, H. J., Lurie, Max B., and Uyei, N. 1927.

The variability of localization of tubercle bacillus in the organs of different animals. III. The importance of the growth of tubercle bacilli as determined by gaseous tension. Am. Rev. Tuberculosis, *15*, 65–87.

Czaplewski. 1895–7. Keimgehalt künstlicher Mineralwasser. Z. f. die ges. Kohlensäureind. Series of articles through several issues in 1895–7.

Dack, Gail M., Starin, W. A., and Werner, Marie. 1927. Growth of Cl. botulinum and Cl. sporogenes in veal infusion broth under reduced pressure. J. Inf. Dis., *40*, 525–532.

Donald, J. R., Jones, C. L., and MacLeon, A. R. M. 1924. The effect of carbonation on bacteria in beverages. Am. J. Pub. H., *14*, 122–128.

Draer. 1897. Z. f. die ges. Kohlensäureind. *3*, 51.

Durrell, L. W. 1924. Stimulation of spore germination by CO_2. Science, *50*, no. 1561, 499.

Eldson, G. D. 1912. The bacteriology of aerated water. Chemical News, *106*, 223, also 247.

Erickson, M. J., and Albert, A. 1922. Cultivation of the gonococcus. J. Inf. Dis., *30*, 268–278.

Fitch, C. P., 1922. The cultivation of Bact. abortus (Bang). J. Inf. Dis., *31*, 233–235.

Foa, C. 1906. L'azione dei gas compressi su la vita dei microorganismi e dei fermenti. Rendiconti Acc. Lincei 5, *15*, sem I, 730, sem II, 53, *Abstract in* Botan. Centr. 1908, *107*, 622–623.

Fränkel, Carl. 1889. Die Einwirkung der Kohlensäure auf die Lebenstätigkeit der Mikroorganismen. Z. f. Hyg., *5*, 332–362.

Frankland, Percy F. 1889. Ueber den Einfluss der Kohlensäure und anderer Gase auf die Entwickelungsfähigkeit der Mikroorganismen. Z. f. Hyg., *6*, 13–17. *Also in* Nature, 1896, *34*, 375–376.

Gates, L. Frederick. 1919. The effect of carbon dioxide in the cultivation of the meningococcus. J. Exp. Med., *29*, 321–328.

Gershenfeld, Louis. 1920. Bacteria in (so-called) soft drinks. Am. Food J., *15*, July, 16–17.

Gillespie, L. J. 1913. The comparative viability of pneumococci on solid and fluid media. J. Exp. Med., *18*, 584–591.

Godlewsky, E. 1892. Zur Kenntnis der Nitrifikation. Anz. Akad. Wissenschaft. Krakow, 408–457, Ibid 1895, 178–192; *also* Centrbl. Bakt., Abt. II, *2*, 458–462. (1896)

Gowda, R. Nagan. 1924. Nitrification and the nitrifying organisms. I. J. Bact., *9*, 251–271.

Grosman, Carl, und Mayerhausen. 1881. Ueber das Leben der Bakterien in Gasen. Arch. ges. Physiol. (Pflüger's), *15*, 248.

Haenle, Oscar. 1905. Bakteriologische Studien über künstliches Selterswasser. Centrbl. f. Bakt., Abt. I Orig., *40*, 609–613. *Also in:* J. pharm. d'Alsace Lorraine, Strassburg, 1905, *32*, 205–211.

Herrold, R. D. 1920. A simplified plate method of partial oxygen tension in the cultivation of the gonococcus. J. Am. Med. Assoc., *74*, 1716.

Hochstetter, M. 1887. Ueber Mikroorganismen im künstlichen Selterswasser nebst einigen vergleichenden Untersuchungen über ihr Verhalten im Berliner Leitungswasser und im destillierten Wasser. Arb. a. d. kais. Gesundh., *2*, 1–29.

Hoffmann, W. 1906. Ueber den Einfluss hohen Kohlensäuredrucks auf Bakterien im Wasser und in der Milch. Arch. f. Hyg., *57*, 379–400.

Huddleson, I. F. 1920. Studies in Infectious Abortion. Mich. Agr. College Exp. Sta. Technical Bulletin *49*, East Lansing.

———. 1921. The importance of an increased carbon dioxide tension in growing Bact. abortus (Bang). Abst. Bact., *5*, 16; *also in* Cornell Vet. 1921, *11*, 210.

Hunziker, O. F. 1924. Facts about carbonated butter. J. Dairy Science, 7, 484–496. (See page 491).

Jones, C. L. 1923. The uses of carbon dioxide I. Can. Chem. and Met., July and August, 7.

Kohman, Ed. F. 1919. The so-called reduced oxygen tension for growing the meningococcus. J. Bact., *4*, 571–584.

Kolbe, Hermann. 1882. Antiseptische Eigenschaften der Kohlensäure. J. prakt. Chem., *26*, 249–255.

Koser, S. A., and Skinner, W. W. 1922. Viability of the colon-typhoid group in carbonated waters and carbonated beverages. J. Bact., 7, 111–121.

Kulp, W. L. 1926. The determination of viable Lactobacillus acidophilus. Science, *64*, no. 1656, 304–306.

Larsen, W. P., Hartzell, T. B., and Diehl, H. S. 1918. The effect of high pressures on bacteria. J. Inf. Dis., *22*, 271–279.

Leone, C. 1886. Untersuchungen über die Mikroorganismen des Trinkwassers und ihr Verhalten in Kohlensäuren Wässern. Arch. f. Hyg., *4*, 168–175.

Liborius, Paul. 1886. Beiträge zur Kenntnis des Sauerstoff-bedürfnisses der Bakterien. Z. Hyg. und Infektionskrankh., *1*, 115–176.

Lieske, Rudolf. 1911. Beiträge zur Kenntnis der Physiologie von Spirophyllum ferrugineum (Ellis) einem typischen Eisenbakterium. Jahrb. f. wissen. Botan., *49*, 91–127.

Lorentz, H. F. 1923. Die Veränderung von Bakterien unter Gasen. Klin. Wochnschrft., *2*, 206–208; *abstract in* J. Am. Med. Assoc., 1923, 80, 1277.

Lubinsky, W. 1894. Ueber die Anaerobiose bei der Eiterung. Centr. Bakt. u. Parasitenk., *16*, 769–775. See page 773.

MacKenzie, Shaw. 1918. Toxic action of carbonic acid and other weak acids on meningococcus. J. Roy. Army Med. Corps, *31*, 1–11.

Masur, B. L. 1926. Zur Biologie des Tuberkelbacillus. Centr. f. Bakt. u. Parasitenk., Abt. I orig., *99*, 46–52.

McAlpine, J. G. and Slanetz, C. A. 1926. Studies on the metabolism of the Bact. abortus-melitensis bronchisepticum-alcaligines group. 1. Nitrogen metabolism. J. Bact., *13*, 11–13.

McKelvey, Chas. E. 1926. Notes on yeast in carbonated beverages. J. Bact., *11*, 98–99.

Melsens, M. 1870. Note sur la vitalité de la levûre de bière. Compt. rend. Ac. Sci., *70*, 629–632.

Meyerhof, Otto. 1916–17. Untersuchungen ueber den Atmungsvorgang nitrifizierender Bakterien. Die Atmung des Nitratbildners und Nitritbildners. Arch. f. ges. Physiol., (Pflüger's) *164*, 353–427, *166*, 240–280.

Moore, B. and Williams, R. S. 1909–11. The growth of the Bacillus tuberculosis and other microorganisms in different percentages of oxygen. Biochem. J., *4*, 177, ibid, *5*, 181.

Morgenroth. 1899. Ueber den Bakteriengehalt der künstlichen und natürlichen Mineralwässer. Z. f. die ges. Kohlensäureind., *5*, 99; *also in* Hyg. Rundschau, *9*, 176.

Neumann, Rudolf. 1897. Studien über die Variabilität der Farbstoffbildung bei Mikrococcus pyogenes α aureus (Staphylococcus pyogenes aureus) und einigen anderen Spaltpilzen. Arch. f. Hyg., *30*, 28–31.

Nourry, Cl. et Michel, C. 1892. Action microbicide de l'acide carbonique. Compt. rend. Ac. Sc., *115*, 959.

Novy, F. G., and Soule, M. H. 1925. Microbic respiration. Respiration of the tubercle bacillus. J. Inf. Dis., *36*, 109–232.

Nowak, Jules. 1908. Le bacille de Bang et sa biologie. Ann. de l'inst. Pasteur, *22*, 541–555.

Noyes, H. A., and Lester, Yoder. 1918. Effect of carbon dioxide gas on bacterial numbers, ammonification and nitrification. Abstr. Bact., *2*, 3 (8).

Pasteur, Louis, et Joubert. 1877. Étude sur la maladie charbonneuse. Compt. rendu Acad. Sci., *84*, 900.

Pfuhl. 1886. Bacterioskopische Untersuchungen im Winter 1884/85. Deut. Militärärzt. Z., *15*, 1–31.

Phelon, H. V., Duthie, Georgiana M., and McLeod, J. W. 1927. The rapid death of meningococcus and gonococcus in oxygenated cultures; the part played by unduly alkaline reaction. J. Path. Bact., *30*, 133–149.

Plastridge, W. N., and Rettger, L. F. 1927. Carbon dioxide and bacterial toxin production: Preliminary report on Diphtheria Toxin. Proc. Soc. Exp. Med. & Biol., *24*, 752–755.

Plummer, J. K. 1916. Some effects of oxygen and carbon dioxide on nitrification and ammonification in soils. Cornell Agr. Exp. Sta. Bull. 384, 303.

Prescott, S. C., and Parker, M. E. 1924. The effect of carbonation on bacteria in commercial ice cream. Cambridge, Mass. 16 pages.

Prucha, M. J., Brannon, J. M., and Ambrose, A. S. 1922. Does carbon dioxide in carbonated milk and milk products destroy bacteria? Cir. 256, Ill. Agr. Exp. Sta., Urbana.

Prucha, M. J., Brannon, J. M., and Ruehe, H. A. 1925. Carbonation of butter. J. Dairy Sci., *8*, 318–329.

Rettger, Leo, F., Winslow, C.-E., and Smith, Arthur H. 1922. Report of an investigation into the effect of freezing ice cream in an atmosphere of carbon dioxide. National Assoc. Ice Cream Dealers.

Rippel, August, und Bortels, Hermann. 1927. Vorläufige Versuche über die allgemeine Bedeutung der Kohlensäure für die Pflanzenzelle. (Versuche an Aspergillus niger.) Biochem. Z., *184*, 237–244.

Rockwell, G. E. 1921. The study of the gaseous requirements for the growth of various bacteria. J. Inf. Dis., *28*, 352–356.

———. 1923. The influence of carbon dioxide on the growth of bacteria. J. Inf. Dis., *32*, 98–104.

———. 1924. An improved method for anaerobic cultures. J. Inf. Dis., *35*, 580–586.

Rockwell, George E., and Highberger, J. H. 1926. Carbon dioxide as a factor in the growth of the tubercle bacillus and of other acidfast organisms. J. Inf. Dis., *38*, 92–100.

———. 1927. The necessity of carbon dioxide for the growth of bacteria, yeasts and molds. J. Inf. Dis., *40*, 438–445.

Rockwell, G. E., and McKann, C. F. 1921. The growth of the gonococcus in various gaseous environments. J. Inf. Dis., *28*, 249–258.

Rogers, L. A. 1914. The preparation of dried cultures. J. Inf. Dis., *14*, 100–123. See page 120.

Ruediger, E. H. 1919. Exclusion of air in the

cultivation of the gonococcus. J. Inf. Dis., *24*, 376–377.

Sabrazès, J., et Bazin, Ed. 1893. L'acide carbonique à haute pression peut-il être considéré comme un antiseptique puissant? Compt. rend. Soc. Biol., *5*, 909–914.

Scala e Sanfelice. 1891. Azione dell'acido carbonico disciolto nelle acque potabile su alcuni microorganismi pathogeni. Centr. f. Bakt. u. Parasitenk., *9*, 110–113.

Schaffer and Freudenreich. 1891. Pressure and microbes. Ann. de Micrographie, *4*, 105–119.

Sierakowski, S., and Zajdel, R. 1924. Ueber die Rolle des Kohlensäure anhydrids in Bakterienkulturen. Biochem. Z., *152*, 111–115. *Also in* Compt. rend. Soc. de Biol., *90*, 1108–1110.

Sirotinin. 1888. Einige Versuche über die Einwirkung der Kohlensäure auf das Wachstum von Bakterien. Z. f. Hyg., *4*, 286–288.

Slater, Charles. 1893. A bacteriological investigation of artificial mineral waters. J. Path. and Bact., *1*, 468–488.

Smith, Theobald. 1924. Some cultural characters of Bacillus abortus (Bang) with special reference to CO_2 requirements. J. Exp. Med., *40*, 219–232.

———. 1926. Variations in CO_2 requirements among bovine strains of Bacillus abortus. J. Exp. Med., *43*, 317–325.

Sohnke. 1886. Z. f. Mineralwasserfabrikation. *22*, 23.

Starkey, Robert L. 1925. Concerning the physiology of Thiobacillus thiooxidans, an autotrophic bacterium oxidizing sulphur under acid conditions. J. Bact., *10*, 135–165

St. John, J. H. 1919. Oxygen tension in its relation to the meningococcus. Med. Record, *95*, 184–186.

Stokes, W. R. 1920. Bacteriological examination of soft drinks. Am. J. Pub. Health, *10*, 308–311.

Swartz, E. O., and Davis, D. M. 1920. Method of cultivating the gonococcus. J. Am. Med. Assoc., *75*, 1125.

Szpilman, Josef. 1880. Ueber das Verhalten der Milzbrand Bacillen in Gasen. Hoppe-Seyler Z. f. physiol. Chem., *4*, 350.

Torrey, J. C., and Buckell, George T. 1921. Cultural methods for the gonococcus. J. Inf. Dis., *31*, 125–126.

Valley, George, and Rettger, Leo F. 1925. Preliminary report on the influence of carbon dioxide on bacterial growth. Abstracts Bact., *9*, 344–345.

———. 1926. Carbon dioxide requirements of bacteria. J. Bact., *11*, 78.

———. 1927. The influence of carbon dioxide on bacteria. J. Bact., *14*, 101–137.

Van Slyke, L. L., and Bosworth, A. W. 1907. Effect of treating milk with carbon dioxide gas under pressure. N. Y. (Geneva) Agr. Exp. Sta. Bull. *292*, 371–384.

Vinogradsky, M. S. 1890. Recherches sur les organismes de la nitrification II. Ann. de l'Inst. Pasteur, *4*, 257–275; *also* Centr. Bakt. u. Parasitenk., Abt. II, *5*, 329, 377, 429.

Waksman, S. A., and Starkey, R. L. 1922. Carbon assimilation and respiration of autotrophic bacteria. Proc. Soc. Exp. Med., *20*, 9–14.

———. 1923. On the growth and respiration of sulphur oxidizing bacteria. J. Gen. Physiol., *5*, 285–310.

Wherry, Wm. B., and Ervin, D. M. 1918. The necessity of carbon dioxide for the growth of B. tuberculosis. J. Inf. Dis., *22*, 194–197.

Wherry, Wm. B., and Oliver, Wade W. 1916. Adaptation to certain tensions of oxygen as shown by gonococcus and other parasitic and saprophytic bacteria. J. Inf. Dis., *19*, 288–298.

Young, C. C., and Sherwood, N. P. 1911. The effect of the environment of carbonated beverages on bacteria. J. Ind. and Eng. Chem., *3*, 495.

THE EVOLUTIONARY SIGNIFICANCE OF THE PROTOZOAN PARASITES OF MONKEYS AND MAN

By ROBERT HEGNER

Department of Protozoology, Johns Hopkins University School of Hygiene and Public Health

INTRODUCTION

PARASITISM is one of the many types of association that exist between different species of living organisms. When used in a narrow sense the term implies injury to one member of the association, the host, and benefit to the other, the parasite; but as generally employed the term parasite is given to any animal or plant that lives on or within and at the expense of another animal or plant. Such associations are, at least in some instances, actually beneficial to the host, as Cleveland (1926) has shown in the case of termites (white ants) and their intestinal flagellates. The latter digest the cellulose in the wood eaten by the termites, thus making it available for the nourishment of these insects; otherwise the termites would starve to death in the midst of an abundance of food. Many groups in the animal kingdom contain parasitic species, and the evidence is overwhelmingly in favor of the view that the parasitic habit has evolved from the free-living mode of existence and has arisen many times within each group. Parasites are particularly abundant among the Protozoa, flat worms (Platyhelminthes), round worm (Nemathelminthes), and Arthropoda (insects and arachnids).

Protozoa and Primates belong to the first and last phyla in the animal kingdom when these are arranged in an evolutionary series. Both groups have been very successful in the struggle for existence, since one of the primates, Man, is now the dominant species on the surface of the earth, and the Protozoa probably excel in number of species and in number of individuals every other group of animals. These two types of animals are not only able to live and reproduce under the complex conditions that now exist in the world, but many of them live together as parasite and host. The results of this type of parasitism are often beneficial to the protozoa and may or may not be harmful to the primates.

The monkeys and man are included in the order Primates in the Class Mammalia. One difficulty in any discussion of the primates is that of nomenclature; so many common and scientific names have been proposed for the various species that much confusion exists and it is often impossible to determine which species is being referred to. The large *Review of the Primates* by Elliot (1913) is not very satisfactory from the standpoint of classification but is used as a basis by many writers. Recently Stiles and Orleman (1927) have prepared a bulletin on *The Nomenclature for Man, the Chimpanzee, the Orang-utan, and the Barbary Ape*, and the names of the other primates that are known to be parasitized by Protozoa are soon to be presented according to modern methods of nomenclature in another

bulletin. In the meantime the writer has used the scientific and common names employed in the current literature.

The Protozoa are usually separated into four classes, the members of which can be distinguished by the presence or absence of locomotor organs and the character of these when present. The Sarcodina throw out temporary cytoplasmic projections known as pseudopodia; the Mastigophora possess one or several threadlike flagella; the Sporozoa have no locomotor organs; and the Infusoria are covered more or less completely with minute hair-like cilia. The Sporozoa are all parasitic, but the other three classes include both free-living and parasitic species. Protozoa are all very small; a few of them can be seen with the naked eye, especially when large numbers are crowded into a small area, but most of them are microscopic in size. Elaborate methods have been evolved during the course of years for their study, and it is now possible to cultivate not only free-living species, but also many of the parasitic forms, in test tubes in artificial media. Much has been learned by the use of laboratory animals; and cross-infection experiments have revealed many data regarding the environmental factors necessary for their growth and reproduction.

Both monkeys and man are parasitized by certain members of all four classes of Protozoa. For convenience we may recognize two types of protozoan parasites, (1) intestinal protozoa, including also those that live in the mouth, stomach, vagina, and urinary tract, and (2) blood-inhabiting protozoa. The former include representatives among the amoebae (figs. 1–4), flagellates (figs. 5–9), coccidia and ciliates (figs. 10–11). Many protozoa have been described from human fecal material that are not inhabitants of the intestine but were either ingested in food or drink and had passed through the digestive tract in a viable condition, or had found their way into the feces after they were passed: these are known as coprozoic protozoa. The blood-inhabiting protozoa of primates consist principally of certain flagellates (figs. 12–13) and malarial organisms (figs. 14–19). Besides the protozoa belonging to the two large groups mentioned, are the sarcosporidia (Sporozoa) that parasitize muscle, and a few others of doubtful validity.

One of the most fascinating problems in protozoology is that of host-parasite specificity (Hegner, 1926a). Why is it that one species of protozoon is able to live in one species of animal but not in another nearly related species? This appears to be true of most species of human parasites. Does the ability of a protozoon to live in two species of animals indicate that the latter are closely related? This is a problem of great interest and importance, since evidence of the organic evolution of hosts may be inferred from the character of their parasites. It is mainly with this point in mind that this article has been prepared. A comparison is presented in the following pages of the amoebae, intestinal flagellates, intestinal ciliates, trypanosomes, leishmanias, malarial parasites, and certain other species of protozoa that live in monkeys and man. This requires the use of many scientific names, both of the protozoa and of their monkey hosts; but the accompanying figures may serve to make these intelligible to readers who are not biologists. This is followed by a brief résumé of the species that occur in the two types of hosts, and is concluded with a statement regarding the significance of these parasites in the study of genetic relationships of hosts as applied to monkeys and man.

Hundreds of different species of intestinal protozoa have been reported from man, but careful study indicates that most of these are not separate species. On the basis of our present knowledge we may recognize six species of amoebae (Sarcodina), seven species of flagellates (Mastigophora), one species of coccidium (Sporozoa), and one species of ciliate (Infusoria). All of these protozoa appear to be world wide in their distribution, and no differences as regards racial susceptibility have been established with certainty; resistance of the individual, however, appears to increase with age. The location of these species in the body and the approximate incidence of infection among the general population are as follows:

	per cent
Mouth:	
Endamoeba gingivalis (Amoeba)..........	50
Trichomonas buccalis (Flagellate).........	10–30
Small intestine:	
Giardia lamblia (Flagellate)...............	10
Isospora hominis (Coccidium).............	?
Large intestine:	
Endamoeba histolytica (Amoeba)..........	10
Endamoeba coli (Amoeba)...........	50
Endolimax nana (Amoeba)..........	25
Iodamoeba williamsi (Amoeba)..........	10
Dientamoeba fragilis (Amoeba)..........	?
Trichomonas hominis (Flagellate).........	5–20
Chilomastix mesnili (Flagellate).........	10
Embadomonas intestinalis (Flagellate).....	?
Tricercomonas intestinalis (Flagellate).........	?
Balantidium coli (Ciliate)............	?
Vagina and urinary tract:	
Trichomonas vaginalis	

Two points of particular interest brought out by these data are the high incidence of infection with certain species and the differences in incidence among the various species. It is evident that man is very susceptible to infection with such species as *Endamoeba gingivalis*, *Trichomonas buccalis*, *Endamoeba coli*, and *Trichomonas vaginalis*. It is also obvious that these species have little difficulty in gaining entrance to the human body. The two species that inhabit the oral cavity are no doubt frequently passed from mouth to mouth during kissing, and probably no one escapes contamination with these protozoa. The intestinal species are mostly transmitted in the cyst stage and the high incidence of infection indicates that contamination of food and drink with feces containing cysts is frequent and widespread.

The facts regarding the pathogenicity of human intestinal protozoa may be stated briefly as follows. *Endamoeba histolytica* is pathogenic especially in tropical and semitropical regions; it is the etiological agent of amoebic dysentery and amoebic liver abscess, and is frequently fatal. Most of those infected with this species are carriers and do not exhibit symptoms. *Endamoeba coli* and *Endamoeba gingivalis* may be pathogenic but this has not yet been definitely proven. The other species of amoebae appear to be harmless. Of the flagellates, *Giardia lamblia*, *Trichomonas hominis*, and *Chilomastix mesnili*, have been accused of causing "flagellate diarrhea;" but their actual relation to the diarrheic condition is not certain; *Trichomonas buccalis* seems to be more frequent in persons suffering from pyorrhea, acute gingivitis, or abscessed teeth than in normal mouths (Hogue, 1926; Hinshaw, 1926), but are probably not responsible for these diseases; *Trichomonas vaginalis* is more common when the vaginal mucus is in an abnormal condition but its relation

species of flagellates are both rare and apparently harmless. The human coccidium, *Isospora hominis*, is always pathogenic but is rare and the diarrhea it produces is of short duration and not lethal. The ciliate, *Balantidium coli*, is the agent of balantidial dysentery, which may be fatal to the host, but is not of frequent occurrence.

The blood-inhabiting protozoa of man are three species of trypanosomes (Mastigophora), three species of leishmanias (Mastigophora), and three species of malarial parasites (Sporozoa). These are all pathogenic and of great importance where they occur, but are more or less local in their distribution. The trypanosomes cause Gambian sleeping sickness (*Trypanosoma gambiense*) and Rhodesian sleeping sickness (*T. rhodesiense*) in tropical Africa, and Chagas' disease (*T. cruzi*) in certain parts of South America. The leishmanias cause kala-azar (*Leishmania donovani*) in parts of Asia, Africa and Europe, oriental sore (*L. tropica*) in certain regions of Asia and Africa, and South American leishmaniasis (*L. braziliensis*) in South America. The three species of malarial parasites, *Plasmodium vivax* of tertian malaria, *P. malariae* of quartan malaria, and *P. falciparum* of estivo-autumnal malaria, occur in tropical and semitropical regions throughout the world.

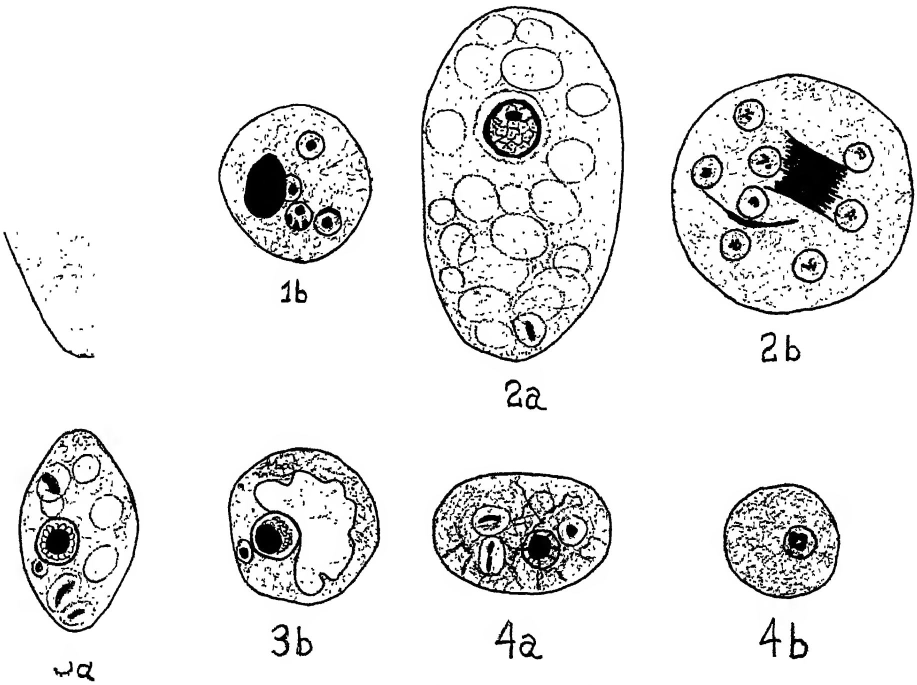
Protozoa were first discovered in man by Leeuwenhoek in 1681. Among the many protozoa described by this famous Dutch microscopist were flagellates, that we now know as giardias, which he encountered in his own stools. However, free-living species were the first to receive attention from biologists, and only comparatively recently have parasitic species attracted investigators. Such discoveries as that of the parasite of amoebic dysentery by Loesch in 1873 (Loesch, 1875), of the malarial parasite by Laveran in 1880 and of a human trypanosome by Forde in 1901 (Forde, 1902) stimulated thousands of investigators to enter the field of protozoology and has resulted in a large body of knowledge regarding the parasitic species, especially those that live in man and domesticated animals.

Protozoa were first reported from monkeys about the year 1899 when Laveran named a species of malarial parasite, *Plasmodium kochi*, that Koch had discovered in 1898 in Africa. Trypanosomes were noted in the chimpanzee by Ziemann in 1902; the ciliate, *Balantidium coli*, in orang-utans by Brooks in 1903; amoebae in a macaque, *Macacus pileatus*, by Castellani in 1908; and intestinal flagellates in another species of macaque, *Macacus cynomolgus*, by Noc in the same year. During the succeeding twenty years protozoa resembling almost every species known to live in man have been recorded from monkeys. It was not, however, until about 1920 that investigators attempted to determine by experiment whether the protozoa of monkeys and man belong to the same or to different species. Recently many cross-infection and cultivation experiments have been carried out, but we are still very much in doubt regarding the host-parasite specificity of monkey protozoa.

AMOEBAE OF MONKEYS AND MAN

At least eleven species of amoebae belonging to three genera have been described from monkeys. Nine of these have been placed by their discoverers in the genus *Endamoeba* and one each in the genera *Endolimax* and *Iodamoeba*. The endamoebae all fall into two types that correspond to two of the common species living in man, namely, *Endamoeba coli* with cysts containing 8 nuclei (fig. 2b), and *E. histolytica* with cysts possessing

4 nuclei (fig. 1b). *Endamoeba nuttalli* of Castellani (1908) resembles *E. histolytica* of man both in the active trophozoite stage and in the character of its cysts. It seems probable that if *E. nuttalli* is a species distinct from *E. histolytica*, then of Old World and New World monkeys. The amoebae to which Castellani gave the name *E. nuttalli* were found by him in a liver abscess in a macaque (*Macacus pileatus*) in Colombo, Ceylon; and Suldey (1924) reported typical amoebic dysentery



AMOEBAE OF MONKEYS AND MAN

FIG. 1a. *Endamoeba duboscqi*. Active, trophozoite stage of histolytica-type o amoeba from the rhesus monkey, *Macacus rhesus*. (After Mathis.)
FIG. 1b. *Endamoeba duboscqi*. Cyst stage containing four nuclei and large chromatoid body. (After Mathis.)
FIG. 2a. *Endamoeba pitheci*. Active, trophozoite stage of coli-type of amoeba from a monkey. (After Hegner and Taliaferro.)
FIG. 2b. *E. pitheci*. Cyst stage containing eight nuclei and chromatoid bodies. (After Hegner and Taliaferro.)
FIG. 3a. *Iodamoeba kueneni*. Active, trophozoite stage from a monkey resembling similar stage of *Iodamoeba williamsi* of man. (After Hegner and Taliaferro.)
FIG. 3b. *Iodamoeba kueneni*. Cyst stage from a monkey. (After Hegner and Taliaferro.)
FIG. 4a. *Endolimax nana*. Active, trophozoite stage from man. (After Hegner and Taliaferro.)
FIG. 4b. *Endolimax nana*. Cyst stage from man. (After Hegner and Taliaferro.) All figures drawn at a magnification of about 2000 diameters.

the other four species described from monkeys belong to that species (*E. nuttalli*). These histolytica-like amoebae have been noted in the gorilla (Wenyon, 1926), chimpanzee (Suldey, 1924; Deschiens, 1927), and various other species in a three year old captive chimpanzee. Most of the infected monkeys, however, appear to be carriers, that is, the amoebae are present in the intestine, where they grow, multiply and form cysts, but the host-parasite relations are such that symp-

toms do not appear. In these respects this type of monkey amoeba resembles *E. histolytica* of man; the latter is present in about ten per cent of healthy human beings in the general population but occasionally gives rise to dysentery and liver abscesses. No morphological differences have yet been found for distinguishing between *E. nuttalli* of monkeys and *E. histolytica* of man.

Are monkeys susceptible to infection with *E. histolytica* from man, and can man be infected with *E. nuttalli* from monkeys? Evidence on cross-infection is available from both epidemiological observations and from laboratory experiments. In the first place most of the monkeys in which amoebae have been found had been in captivity, and hence associated with human beings for various lengths of time. They may thus have become infected with cysts from man. As noted above, the infected chimpanzee reported by Suldey was a captive animal. Mathis (1913) described an infection with a histolytica-like amoeba (*Endamoeba duboscqi*, figs. 1a, 1b) in a macaque (*Macacus rhesus*) that had been in Germany for 16 years; in this case an original infection must have lasted for that length of time or else the monkey became infected with human amoebae while in captivity, or possibly with amoebae from other monkeys with which it was associated. On the other hand, McCarrison (1919), as a result of studies on 36 young monkeys (*Macacus sinicus*) in India, states that "monkeys in a wild state in S. India may be carriers of *E. tetragena* (*histolytica*)." Successful attempts to infect monkeys by inoculating them with trophozoites or cysts of *E. histolytica* from man have been reported by several investigators. Thus Franchini (1912) claims to have infected a monkey (species not given) with *E. histolytica* per rectum. Kessel (1926a) fed cysts of *E. histolytica* to two amoeba-free monkeys (*Macacus*) and recovered trophozoites and cysts from their feces racially indistinguishable from the type of amoebae fed to them, and, after autopsy, found similar specimens in histological sections.

There is also epidemiological evidence that the histolytica-like amoebae from monkeys are infective to man; for example, infections with this type of amoeba in three individuals in Baltimore have been traced to a colony of rhesus monkeys maintained for experimental purposes.

The laboratory animals most susceptible to infection with *E. histolytica* from man seem to be young cats of about 500 grams in weight. Infections in kittens have been established by feeding them cysts, and by injecting trophozoites or cysts (Hoare, 1925) into the colon per rectum. Mello (1923) reports the infection of kittens by the rectal injection of dysenteric feces of monkeys (*Macacus sinicus*). Dobell (1926) likewise succeeded in infecting kittens with histolytica-like amoebae from monkeys (*Macacus rhesus* and *M. sinicus*) but states that the resulting dysentery differs from that produced by *E. histolytica* from man. The infection of two cats, 6 and 7 months old respectively, by rectal injections of feces containing cysts of naturally infected monkeys was obtained by Kessel (1926a). Two months after injection the cats at autopsy were found to contain trophozoites in the upper colon and cecum and also in the tissues of the intestinal wall. In a later paper Kessel (1927) reports the successful infection of 8 of 13 kittens with trophozoites or cysts of histolytica-like amoebae from monkeys; 6 of the kittens succumbed to dysentery of the type induced in these animals by *E. histolytica* from man.

The methods introduced by Boeck and Drbohlav (1925) for cultivating human

amoebae have also been used for the cultivation of amoebae from monkeys. Dobell (1926, 1927) has carried on cultures of the histolytica-like amoebae of monkeys for many months and finds no differences between their reactions in culture and those of *E. histolytica* from man. Kessel (1926a) and Vogel (1927) report similar results.

The data available lead to the following conclusions regarding *Endamoeba histolytica* from man and the histolytica-like amoebae from monkeys: (1) The histolytica-like amoebae of monkeys, which have been given at least five distinct specific names, all belong, probably, to one species, *Endamoeba nuttalli* Castellani 1908, if they are not identical with *E. histolytica*. (2) There are no satisfactory morphological characteristics by means of which the histolytica type of amoebae of monkeys and man can be distinguished. (3) Histolytica-like amoebae have been reported principally from captive monkeys that may have become infected by the ingestion of food or drink contaminated with cysts from man. (4) Amoebic dysentery and amoebic liver abscess in monkeys resemble these diseases in man. (5) Most monkeys and men infected with histolytica amoebae are carriers. (6) Monkeys have been successfully infected with *E. histolytica* from man. (7) Human beings seem to have become infected by association with monkeys. (8) Kittens may be infected by amoebae from both monkeys and man. (9) Histolytica amoebae from monkeys and man exhibit similar reactions under cultivation in artificial media. (10) Either the histolytica-like amoebae of monkeys belong to the species *Endamoeba histolytica* or else we have not yet discovered differences sufficient to distinguish one from the other.

The situation as regards *Endamoeba coli* of man and the coli-like amoebae of monkeys is similar to that of *E. histolytica*, but not so much evidence is available. Brumpt, in 1909, reported amoebae with eight-nucleated cysts from three specimens of *Macacus sinicus*. Three years later, Prowazek (1912) gave the name *Endamoeba pitheci* (figs. 2a, 2b) to an amoeba with an eight-nucleated cyst that he obtained from a young orang. New specific names have since been given to three other coli-like amoebae found in other species of monkeys (Mathis, 1913; Macfie, 1915; Mello, 1923). There is little evidence that these are actually separate species, and they probably all belong to the species *E. pitheci* if they are not identical with *E. coli* from man. Kessel (1924, 1927) has succeeded in infecting monkeys with *E. coli* from man and both Dobell (1926) and Kessel (1927) have cultivated the coli-like monkey amoeba in vitro. At the Pasteur Institute in Paris, Deschiens (1927) found coli-like amoebae in 5 of 7 chimpanzees and successfully infected a young chimpanzee and a *Macacus* monkey with them; his attempt to infect a cat proved negative as did a similar attempt by Brumpt (1909b). Apparently, therefore, there is no good evidence that the coli-like amoebae of monkeys differ in species from *E. coli* in man.

Amoebae of the genus *Endolimax* (figs. 4a, 4b) have been reported from monkeys by only two investigators. Brug, in 1923, found in an old laboratory monkey (*Macacus cynomolgus*) an amoeba morphologically identical with *Endolimax nana* from man, to which he gave the name *Endolimax cynomolgi*. The second record is that of Deschiens (1927) who reported it from 3 of 7 chimpanzees, from 2 of 9 macaques, and from 2 *Cercopithecus* monkeys at the Pasteur Institute in Paris. He transferred the infection from chim-

panzees to macaques and from one macaque to another. Infections in monkeys with *Endolimax nana* from man have been reported by Kessel (1927). From these meager data it seems possible and even probable that the *Endolimax* of monkeys and man are of the same species.

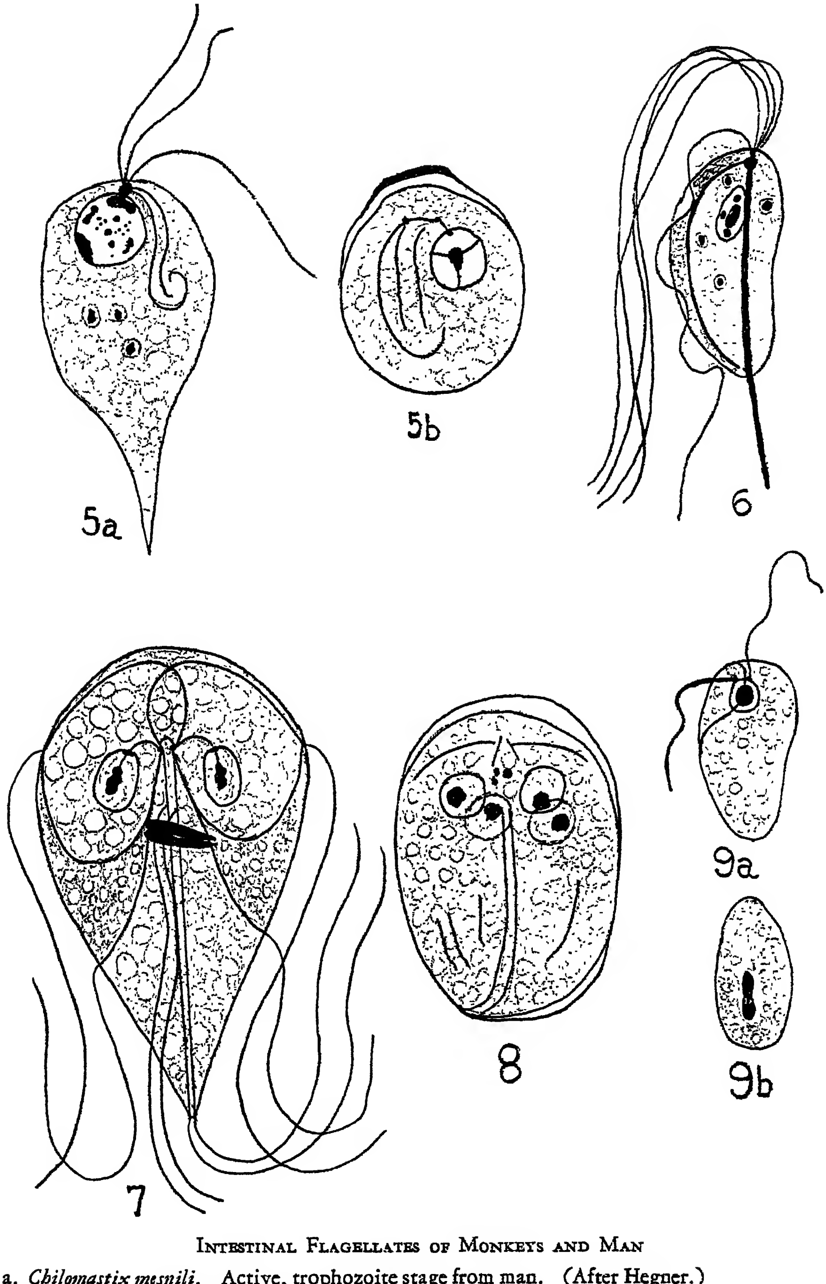
Iodamoebae (figs. 3a, 3b) were first noted in monkeys (*Macacus cynomolgus*) by Brug in 1921; he believed them to be *Endolimax* and gave them the specific name *kueneni*, but his descriptions and figures indicate that they belong to the genus *Iodamoeba*. Since then iodamoebae have been reported from monkeys by Hegner and Taliaferro (1924, in *Cebus variegatus*), Kessel (1924, 1927, in *Macacus*), Wenyon (1926, in the gorilla) and Smith (1928, in *Macacus rhesus*). Recently specimens were found in the writer's laboratory in the intestine of a chimpanzee. Kessel (1924) claims to have infected both of two *Macacus* monkeys with cysts of *Iodamoeba* from man, and Smith (1928) could find no differences between excystation in iodamoebae from man and from *Macacus* monkeys when cysts were fed to guinea-pigs. Brug (1921) states that the cysts of *Iodamoeba kueneni* possess a darkly staining area not present in cysts from man, but it does not seem probable that this characteristic is constant. As in the case of *Endolimax* the conclusion is reached that the iodamoebae of monkeys and man have not yet been shown to belong to different species.

Two species of amoebae that live in man have not yet been reported from monkeys so far as known to the writer. These are *Endamoeba gingivalis*, which inhabits the mouth, and *Dientamoeba fragilis* of the intestine. Smears and cultures from the mouths of many monkeys have been examined in the writer's laboratory for *E. gingivalis* but without success. *Dientamoeba fragilis* is rare in man and may probably live in monkeys but has not been found thus far. Kessel (1924) claims to have found in *Macacus* monkeys amoebae indistinguishable from *Councilmania lafleuri*, a form that Kofoid and Swezy (1921) described as a new genus and species from man but that is believed by many protozoologists to be *Endamoeba coli*, and reports the successful infection of two monkeys with cysts of *C. lafleuri* from man. None of the other doubtful species of amoebae that have been described from man have been encountered in monkeys.

INTESTINAL FLAGELLATES OF MONKEYS AND MAN

Of the seven species of intestinal flagellates that live in man three belong to the genus *Trichomonas* and the other four to the genera *Chilomastix*, *Giardia*, *Embadomonas*, and *Tricercomonas*. An eighth species of doubtful validity is *Enteromonas hominis*. The trichomonads, *Chilomastix*, and *Giardia* are relatively common (see page 227), whereas *Embadomonas* and *Tricercomonas* are rare. Representatives of all of these genera, with the exception of *Tricercomonas*, have been reported from monkeys. The trichomonads of man occur in the intestine (*Trichomonas hominis*), in the mouth (*T. buccalis*) and in the vagina (*T. vaginalis*). Intestinal and vaginal trichomonads occur in monkeys, but the mouth inhabiting type has not been found, although thorough search has been made for it in the writer's laboratory.

Vaginal trichomonads have been reported from monkeys only once (Hegner and Ratcliffe, 1927); these were given the name *Trichomonas macacovaginae* (fig. 6). Trichomonads from the intestine of *Macacus* monkeys when grown in culture and injected into the vagina of uninfected monkeys appeared in 4 of 6 cases to set up at least temporary infections. These



INTESTINAL FLAGELLATES OF MONKEYS AND MAN

FIG. 5a. *Chilomastix mesnili.* Active, trophozoite stage from man. (After Hegner.)
FIG. 5b. *Chilomastix* sp. Cyst stage from a monkey. (After Hegner.)
FIG. 6. *Trichomonas macacovaginae.* Active, trophozoite stage from the vagina of a monkey. (After Hegner and Ratcliffe.)
FIG. 7. *Giardia lamblia.* Active trophozoite stage from man. (After Hegner.)
FIG. 8. *Giardia* sp. Cyst stage from a monkey. (After Hegner.)
FIG. 9a. *Embadomonas intestinalis.* Active, trophozoite stage from man. (After Hegner and Taliaferro.)
FIG. 9b. *Embadomonas intestinalis.* Cyst stage from man. (After Hegner and Taliaferro.) All figures drawn at a magnification of about 4000 diameters.

experiments furnish evidence that vaginal and intestinal trichomonads may belong to one species and that vaginal infections are brought about by contamination with fecal material (Hegner, 1928). No attempts have been made to infect monkeys with vaginal trichomonads from man or vice versa. Morphologically the trichomonads from these two hosts are indistinguishable.

Intestinal trichomonads have been noted in monkeys by Noc (1908) in a specimen of *Macacus cynomolgus*, which was also infected with amoebae and with the ciliate, *Balantidium coli*, and was suffering from dysentery; by Brumpt (1909b) in *Macacus sinicus* monkeys, one of which was dysenteric; by Greig and Wells (1911) in Indian monkeys (*Macacus* sp.); by Prowazek (1912) and Mello (1923) in young orangs; and by Dobell (1926), Hegner and Ratcliffe (1927), Kessel (1927), Branch and Gay (1927), and Deschiens (1927). Although these trichomonads seem to possess no morphological characteristics by means of which they can be separated from human intestinal trichomonads, Deschiens (1927) has proposed the name *Trichomonas anthropopitheci* for specimens he observed in captive chimpanzees. Deschiens cultivated this form in vitro but failed to infect a human being who ingested the cultures. Various other investigators have also cultivated the intestinal trichomonads from monkeys. As noted above, the writer (Hegner, 1928) apparently set up infections in the vagina of rhesus monkeys with cultures of intestinal trichomonads from the same species of host. Kessel (1924) claims to have infected one of two monkeys by feeding them human intestinal trichomonads, and also infected kittens by mouth and by rectum with intestinal trichomonads from both man and monkeys (Kessel, 1926b, 1927). Diarrhea accompanied by great numbers of trichomonads has been described in monkeys, but whether this so-called "flagellate diarrhea" is due to the presence of these organisms is, as in cases of flagellate diarrhea in man, still to be proved.

The first report of *Chilomastix* (=*Macrostoma*) (fig. 5a) from a monkey is that of Prowazek (1912), who found it along with amoebae and trichomonads (see above) in a young orang. Bach (1923) next observed both cysts and trophozoites in an old captive monkey that was also infected with amoebae of the histolytica type (see above). Hegner (1924) reported cysts (fig. 5b) from *Cebus apella* of South America and Kessel (1924) from *Macacus* monkeys of China. Cysts of a *Chilomastix* (*C. mesnili* var. *simiae*), obtained by Deschiens (1926) from the chimpanzee and from *Macacus sinicus*, when fed to young *M. sinicus* monkeys brought about infection in from 15 to 30 days. Kessel (1924) claims to have infected both of two monkeys by feeding them *Chilomastix* from man. Further observations and experiments are necessary before it can be stated with certainty whether *Chilomastix* from monkeys and man belong to the same or to different species.

Giardias were first described in a monkey (*Cebus caraya*) by Fonseca (1915) in South America. They were next reported by the writer (Hegner, 1924) from another South American monkey, *Ateleus geoffroyi*. Wenyon (1926) observed cysts in a young *Cercopithecus* monkey from West Africa, and Deschiens (1927) records giardias in one *Macacus* and one *Cercopithecus* monkey and succeeded in transmitting them from one macaque to another. Deschiens failed to infect cats with the monkey giardias and Kessel (1924) failed to infect *Macacus* monkeys with giardias from man. These data show that giardias are widespread in monkeys but do not

settle the question of specificity of either parasite or host.

The literature contains two records of *Embadomonas* in monkeys. Fonseca (1917) describes specimens from a South American monkey, *Cebus caraya*, which he considers a new species, *E. wenyoni*, on the basis of differences in the type of division between it and the human form, *E. intestinalis;* that it is a new species seems very doubtful. The second reference is that of Kessel (1927) who found *Embadomonas* in *Macacus* monkeys in China and cultivated them in vitro.

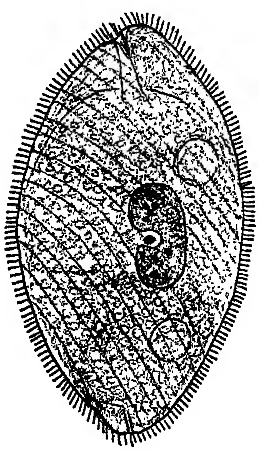


FIG. 10. BALANTIDIUM SP. ACTIVE, TROPHOZOITE STAGE OF CILIATE FROM A MONKEY (×1200) (After Hegner and Holmes)

Enteromonas is mentioned by Dobell (1926) as one of the intestinal flagellates that he found and cultivated from *Macacus* monkeys, but no description of the organism is given.

INTESTINAL CILIATES OF MONKEYS AND MAN

The only ciliate that is known with certainty to occur in man is *Balantidium coli*. Two genera of ciliates are intestinal inhabitants of monkeys, *Balantidium* (fig. 10) and *Troglodytella* (fig. 11). The balantidia are supposed to belong to the same species as that in man and pig, *Balantidium coli*, and are possibly the same as that in the guinea-pig (Scott, 1927). Two species and one variety of *Troglodytella* have been given names; *T. abrassarti* and *T. abrassarti acuminata* occur in chimpanzees (Brumpt and Joyeux, 1912; Reichenow, 1917, 1920a), and *T. gorillae* in the gorilla (Reichenow, 1920a).

Balantidium coli is a particularly interesting protozoon because its host-parasite specificity seems to be very weak. Apparently human beings acquire infection by ingesting cysts from pigs, a large proportion of which are parasitized. Pigs have been infected with balantidia from monkeys (Brumpt, 1909a); and monkeys have been infected with cysts or trophozoites or both from man or pig when fed to them or injected per rectum (Walker, 1913). Two attempts made by Ziemann (1925) to infect himself by swallowing balantidia from chimpanzees were unsuccessful. Scott (1927) has been unable to find any differences of specific rank between the balantidia of guinea-pigs and those of pig and man.

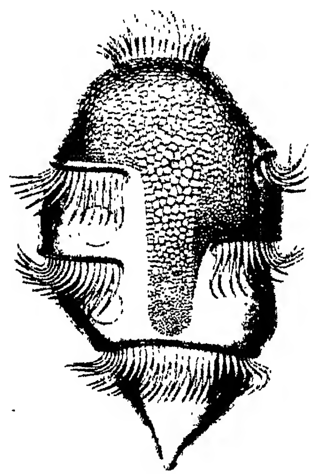
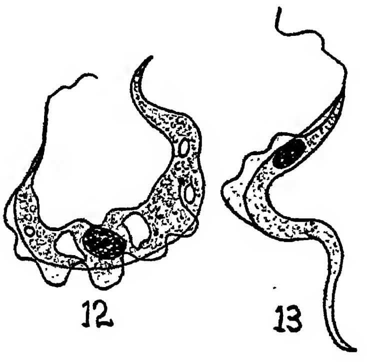


FIG. 11. TROGLODYTELLA ABRASSARTI ACUMINATA. ACTIVE, TROPHOZOITE STAGE OF A CILIATE FROM A CHIMPANZEE (×250) (After Reichenow)

Balantidia were first reported from monkeys by Brooks (1903) in orangs suffering from dysentery in the New York Zoological Gardens; they have since been found in the baboon (Joyeux, 1913), chimpanzee (Christeller, 1922; Ziemann, 1925) and in other Old and New World monkeys (Noc, 1908; Brumpt, 1909a; Hegner and Holmes, 1923). Cunha and Muniz (1927) have given the name *Balantidium aragãoi* to specimens they describe from *Cebus caraya* of Brazil. In about one-half of the cases reported the infected monkeys were diarrheic or dysenteric; the rest of the infected animals were in the carrier state.



TRYPANOSOMES OF MONKEYS

FIG. 12. *Trypanosoma minasense* from a marmoset (×2000). (From Wenyon, after Carini.)

FIG. 13. *Trypanosoma* sp. from a howler monkey (×2000). (From Wenyon, after Brimont.)

TRYPANOSOMES OF MONKEYS AND MAN

The trypanosomes of man are local in their distribution. *Trypanosoma gambiense* and *T. rhodesiense* occur in certain regions of Africa, where they are responsible for Gambian and Rhodesian sleeping sickness. *T. cruzi*, the organism of Chagas' disease, occurs principally in Brazil, but has been reported also from San Salvador, Venezuela, and Peru. These three species of trypanosomes all have animal reservoirs. Several species of armadillos appear to be natural hosts of *T. cruzi* in South America where as many as 50 per cent of these animals have been found infected; the transmitting agent, the bug, *Triatoma megista*, lives in the armadillo burrows (Chagas, 1918). Antelope and other wild game have been accused of serving as reservoirs of *T. gambiense* and *T. rhodesiense* in Africa in association with the tsetse flies which are the transmitting agents. Man and domestic animals, however, are probably more important reservoirs than wild game. The human trypanosomes can be transmitted by blood inoculation or by means of their transmitting insects to various laboratory animals; among the latter are monkeys. Monkeys have also been reported in endemic regions with what seem to have been natural infections with these three species of trypanosomes. For example, Chagas (1924) found specimens in the monkey, *Chrysothrix sciureus*, of Brazil, which, when inoculated into guinea-pigs and dogs, resembled *T. cruzi* both morphologically and in their effects on these hosts. Various investigators have found trypanosomes in monkeys in Africa that they considered identical with human species.

Trypanosomes (figs. 12, 13) have been reported from over a dozen species of monkeys, including the chimpanzee and gorilla and other Old World and New World species. Some of these monkeys seem to have acquired their infections in a wild state. As many as seven new species or varieties have been described from monkeys, but trypanosomes are not easily distinguishable from one another, and the validity of certain of these new species is in doubt.

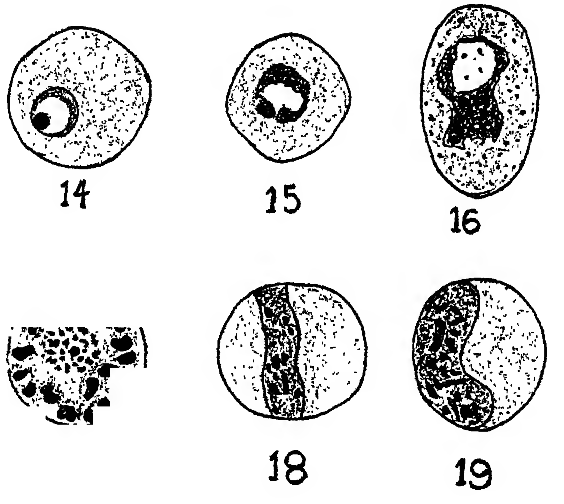
LEISHMANIAS OF MONKEYS AND MAN

The organisms of kala-azar (*Leishmania donovani*), oriental sore (*L. tropica*), and South American leishmaniasis (*L. brazil-

iense) have not been reported from monkeys. The only natural infections thus far discovered have been in dogs and cats. Laboratory monkeys can be infected by the injection of large doses of *L. donovani* grown in culture, but the virus loses its virulence when passed through a succession of animals and finally becomes non-infective. Monkeys may die after several months as a result of infection with *L. donovani*, or may suffer a chronic infection and recover. In some monkeys, as Row (1912), Korke (1914), and Tyzzer and Walker (1919) have shown, cutaneous inoculation with kala-azar material results in skin lesions and not in generalized infections. Monkeys are also susceptible to infection with both *L. tropica* (Nicolle and Sicre, 1908) and *L. braziliense* (Wenyon, 1913). The organisms bring about the production of lesions that resemble those in man, but disappear sooner.

MALARIAL PARASITES OF MONKEYS AND MAN

Malarial parasites were first found in monkeys by Koch in 1898. During the following year Laveran, the discoverer of the malarial parasites of man, discovered similar organisms in *Cercopithecus sabaeus*, to which he gave the specific name *kochi*. Since then malarial parasites (figs. 14–19) have been reported from the chimpanzee, gorilla, orang, baboon, and over a dozen other species of Old World and New World monkeys. At least eight new species have been described, but how many of these are "good" species is still to be determined. Of particular interest is the fact that certain of these parasites in monkeys resemble so closely the three species that occur in man that they are morphologically indistinguishable. Thus *Plasmodium kochi* (fig. 16) is similar to *P. vivax*, the tertian parasite of



MALARIAL PARASITES OF MONKEYS

FIG. 14. *Plasmodium inui*. Ring stage in red blood corpuscle.
FIG. 15. *P. brasilianum*. Young trophozoite.
FIG. 16. *P. kochi*. Older trophozoite (schizont).
FIG. 17. *P. inui*. Segmentation stage (schizogony).
FIG. 18. *P. malariae*. Band-like stage of trophozoite.
FIG. 19. *P. reichenowi*. Crescent-shaped gametocyte.
All figures drawn at a magnification of about 2000 diameters. (From Wenyon. Figs. 14 and 17 after Mathis and Leger; figs. 15 and 16 after Gonder and Gossler; figs. 18 and 19 after Reichenow.)

man, both in the structure of the various stages and in the length of the asexual cycle (48 hours). Other so-called species that resemble *P. vivax* are *P. inui* (figs. 14, 17) (Halberstädter and Prowazek, 1907) and *P. cynomolgi* (Mayer, 1908) from *Macacus* monkeys, *P. bouilliezi* (Leger, 1922) from *Cercopithecus campbelli*, *P. semnopitheci* (Knowles, 1919) from *Semnopithecus entellus*, and *P. pitheci* (Halberstädter and Prowazek, 1907) from the orang. *P. brasilianum* (fig. 15) recorded by Gonder and Gossler (1908) from a Brazilian monkey, *Brachyurus calvus*, resembles *P. malariae*, the parasite of quartan malaria in man, and *P. reichenowi* (fig. 19) (Sluiter, Swellengrebel, and Ihle, 1922) is said to be similar to *P. falciparum* of human estivo-autumnal malaria.

Reichenow (1917, 1920b) has described parasites in chimpanzees and gorillas in the Cameroons that correspond in their various stages to all three of the species that live in man; he believes the organisms of these anthropoid apes to be the same as the human parasites. Similar results were obtained by Blacklock and Adler (1922) from studies of chimpanzees in West Africa. Adler (1923) found parasites resembling *P. falciparum* in 2 of 13 chimpanzees in Sierra Leone. According to Reichenow (1920b) young animals are more highly parasitized than adults, a fact that is true also in human malaria. Malarial infections in monkeys may be acute or chronic as in man. Quinine appears to be effective against *P. kochi* (Gonder and Rodenwaldt, 1910) and *P. inui* (Leger and Bouilliez, 1913). Attempts to infect mosquitoes by feeding them on malarious monkeys have been mostly negative; Blacklock and Adler (1922) failed to infect *Anopheles costalis* on a chimpanzee and Mayer (1908) likewise failed to infect *Culex pipiens* and *Aëdes argenteus* on monkey blood containing *P. inui*, but he observed what he believes were oöcysts in *Anopheles maculipennis*.

Cross-infection experiments indicate that host-parasite specificity among the malarial organisms of monkeys and man is rather rigid. Halberstädter and Prowazek (1907) were able to transfer *P. pitheci* from orang to orang but not to lower monkeys, and *P. inui* from one *Macacus* monkey to another but not to orangs. Mayer (1908) reports successful inoculations of *P. cynomolgi* into *Macacus cynomolgus*, *M. rhesus* and a *Cercopithecus* monkey. Leger and Bouilliez (1912) were able to infect four species of *Macacus*, three species of *Cercopithecus*, and *Papio anabis* with *P. inui*, but failed to infect *C. fuliginosus* and two chimpanzees. Efforts to infect man with blood from monkeys have not succeeded; Gonder and Rodenwaldt (1910) attempted to parasitize two human beings with *P. kochi*, and Blacklock and Adler (1922) failed to infect man by subcutaneous and intravenous injections of malarious blood from chimpanzees. Mesnil and Roubaud (1917, 1920) claim to have infected a chimpanzee with human blood containing *P. vivax*, but attempts by other investigators to transfer infections from man to monkeys have failed (for example, Blacklock and Adler, 1924).

BABESIA OF MONKEYS

So far as is known to the writer there are no representatives of the genus *Babesia* that live in man. Babesias, or piroplasmas, occur especially in cattle, horses, sheep, goats, and dogs, where they may give rise to destructive diseases such as Texas fever in cattle and haemoglobinuric fever in horses. Several apparently authentic cases of *Babesia* in monkeys are on record. Ross (1905) discovered organisms belonging to this genus, to which he gave the specific name *pitheci*, in a species

of *Cercopithecus* in Uganda; and Kikuth (1927) reports the occurrence of similar organisms, also in a *Cercopithecus* monkey. Symptoms of fever and anaemia appeared, and the blood picture resembled that of pernicious anaemia in man.

DOUBTFUL PROTOZOAN PARASITES OF MONKEYS

Many bodies that have been observed in the blood of monkeys have been placed by investigators in various groups of protozoa. Some of these are probably not protozoa and others not even living organisms. In this category may be included the following. Thézé (1916) describes as a *Toxoplasma* bodies found by him in the blood cells of a monkey, *Mycetes seniculus*, in Guiana; A. Leger (1922) names bodies he observed in the blood cells of a rhesus monkey in Annam, *Grahamella rhesi;* and Langeron (1920) and Leger and Bedier (1922) record as *Haemogregarina cynomolgi* and *H. cynomolgi* var. *papio* bodies seen by them in malarious monkeys (*Macacus cynomolgus* and *Papio sphinx*).

GENERA AND SPECIES OF PROTOZOA OF MONKEYS AND MAN

A comparison of the protozoan parasites of monkeys and man is presented in the following table.

	Protozoan Parasites of Man	Protozoan Parasites of Monkeys
	Amoebae	**Amoebae**
1.	*Endamoeba histolytica*	*Endamoeba nuttalli* (= *E. histolytica?*)
2.	*Endamoeba coli*	*Endamoeba pitheci* (= *E. coli?*)
3.	*Endamoeba gingivalis*	....
4.	*Endolimax nana*	*Endolimax cynomolgi* (= *E. nana?*)
5.	*Iodamoeba williamsi*	*Iodamoeba kueneni* (= *I. williamsi?*)
6.	*Dientamoeba fragilis*	....
	Intestinal Flagellates	**Intestinal Flagellates**
7.	*Trichomonas vaginalis*	*Trichomonas macacovaginae* (= *T. vaginalis?*)
8.	*Trichomonas buccalis*	....
9.	*Trichomonas hominis*	*Trichomonas anthropopitheci* (= *T. hominis?*)
10.	*Chilomastix mesnili*	*Chilomastix mesnili* var. *simiae* (= *C. mesnili?*)
11.	*Giardia lamblia*	*Giardia* sp. (= *G. lamblia?*)
12.	*Embadomonas intestinalis*	*Embadomonas wenyoni* (= *E. intestinalis?*)
13.	*Tricercomonas intestinalis*	....
	Intestinal Ciliates	**Intestinal Ciliates**
14.	*Balantidium coli*	*Balantidium aragãoi* (= *B. coli?*)
15.	....	*Troglodytella abrassarti*
16.	....	*Troglodytella abrassarti acuminata*
17.	....	*Troglodytella gorillae*
	Trypanosomes	**Trypanosomes**
18.	*Trypanosoma gambiense*	*Trypanosoma gambiense* (?)
19.	*Trypanosoma rhodesiense*	*Trypanosoma rhodesiense* (?)
20.	*Trypanosoma cruzi*	*Trypanosoma cruzi* (?)
	Leishmanias	**Leishmanias**
21.	*Leishmania donovani*	....
22.	*Leishmania tropica*	....
23.	*Leishmania brasilianum*	....
	Malarial Parasites	**Malarial Parasites**
24.	*Plasmodium vivax*	*Plasmodium vivax* (?)
25.	*Plasmodium malariae*	*Plasmodium malariae* (?)
26.	*Plasmodium falciparum*	*Plasmodium falciparum* (?)
	Other Protozoa	**Other Protozoa**
27.	*Isospora hominis*	....
28.	*Sarcocystis* sp.	....
29.	....	*Babesia pitheci*

All of the protozoa usually recognized by protozoologists as human parasites are listed in the above table. Many species described from monkeys have not been included, however, because of their more or less doubtful validity; this applies particularly to amoebae, trypanosomes, and malarial organisms. Further study may prove that certain of these are specifically distinct, but at present our information regarding them is for the most part too scanty to warrant definite decisions.

The table shows that of the four genera of amoebae that live in man, three are represented among monkey amoebae and the fourth has probably not yet been discovered on account of its rarity. Four of the six well-authenticated species of human amoebae are indistinguishable from four species of amoebae that have been described from monkeys. No amoebae in monkeys have been found corresponding to two of the human species, *Endamoeba gingivalis* of the mouth and *Dientamoeba fragilis* of the intestine. Among the intestinal flagellates of monkeys are five species that are indistinguishable from five of the seven species that live in man; *Trichomonas buccalis* of the mouth and *Tricercomonas intestinalis* of the intestine of man appear to be absent in monkeys. The ciliate, *Balantidium coli*, that lives in man is probably the same species that has been recorded from various species of monkeys. Certain monkeys are infected with a genus of ciliates, *Troglodytella*, of which two species and one variety have been described, that has no representatives in man. All three species of human trypanosomes seem to be present as natural parasites of monkeys. The leishmanias have not been reported from monkeys. Malarial parasites that occur in monkeys resemble the three species that live in man. The coccidium, *Isospora hominis*, of the human intestine and the sarcosporidia that have been reported a few times as muscle parasites of man have not been recorded from monkeys. No parasite corresponding to *Babesia pitheci* of monkeys occurs in man. Thus eleven of the fifteen genera of human protozoa are known to have representatives in monkeys; and seventeen of the twenty-five species of human protozoa have been described from monkeys. One genus of ciliates, *Troglodytella*, and one *Babesia* occur in monkeys but not in man.

GENERA AND SPECIES OF PROTOZOA IN LOWER ANIMALS

The significance of this situation can best be realized by comparing the protozoan parasites of man with those of other lower animals. Such a comparison brings out the fact that although many lower animals are inhabited by protozoa belonging to certain of the same genera as those of man the species can be distinguished without difficulty from human protozoa. Thus the rat is infected with species of intestinal amoebae (e.g., *Endamoeba muris*) and intestinal flagellates (e.g., *Giardia muris*, *Trichomonas muris*), and with blood-inhabiting flagellates (*Trypanosoma lewisi*), but not a single species of the rat is considered by protozoologists to be identical with any human species. Certain genera and many species, however, have been described from rats that do not occur in man. Other mammals whose protozoan parasites are fairly well known, such as cats, dogs, guinea-pigs, pigs, sheep, cattle and horses, are similar to rats in this respect. Spontaneous infections in lower animals with human protozoa have been observed, for example, cats and dogs with amoebiasis apparently due to *Endamoeba histolytica*, and rats with giardiasis as a result of ingesting cysts of the human giardia, *G. lamblia*, and in many of them infections with human protozoa can be

set up in the laboratory, but the lower animals are obviously not natural hosts of human protozoa and only become infected with them in nature under extraordinary conditions (Hegner, 1926a). In susceptible lower animals the course of the infection is often very different from that in monkeys and man. For example, the course of amoebiasis in man usually includes a rather long incubation period, followed by acute dysentery from which the patient recovers in a carrier condition, i.e., the infection continues but is kept down by the resistance of the body below the point at which symptoms appear. Active amoebae only are present during the dysenteric period and chiefly cysts are passed during the carrier period; whereas in cats the incubation period is short, death usually occurs as the result of acute dysentery, and no cysts are formed at any time. In monkeys amoebic dysentery runs a course similar to that in man.

PROTOZOAN PARASITES AND THE GENETIC RELATIONSHIP OF HOSTS

Parasites have been used to a slight extent in the study of the genetic relationships of hosts. Von Jhering in 1902 was among the first to discuss this problem in cases of parasitic worms. He argues that two species of hosts are of common descent if they are parasitized by the same species or nearly related species of parasites. He believes that the close relationship of the parasites indicates that they come from a common ancestor and that the different species of hosts involved descended from an ancestral host that was infected by the ancestral parasite. The most important work of this type involving protozoa is that of Metcalf (1923) on frogs and their ciliate parasites of the family Opalinidae. Metcalf discusses, for example, the distribution of the family Leptodactylidae. These are "frogs" characteristic of two widely separated geographical regions, (1) tropical and semi-tropical America and (2) Australia and Tasmania; they have been reported from no other parts of the world. There are two hypotheses that may account for this discontinuous distribution: (1) there may have been a former connection between Patagonia and Australia by way of Antarctica over which these frogs were continuously distributed, or (2) resemblances of the frogs of America and Australia may be due to convergent or parallel evolution.

Frogs of the family Leptodactylidae contain, in the rectum, opalinid parasites of the genus *Zelleriella*. These parasitic ciliates are present in frogs of this family living in both America and Australia. They are so nearly alike in the frogs of the two regions that they can be separated specifically only with difficulty. It is possible that either the frogs or the opalinid ciliates may have arisen by convergent or parallel evolution. It seems very improbable, however, that both the frogs and opalinids arose in this way. The conclusion is reached that the first hypothesis is correct and that a former land connection existed between Patagonia and Australia by means of which frogs of this family, together with their opalinid parasites, migrated to Australia.

PROTOZOAN PARASITES AND THE GENETIC RELATIONSHIPS OF MONKEYS AND MAN

So far as known to the writer no studies have been made to determine genetic relationships among monkeys with the aid of their parasitic protozoa. In fact, probably not enough is known regarding the protozoa of monkeys to make such a study profitable at present. However, as the data compiled in this paper indicate,

the protozoan parasites of monkeys and man belong for the most part to the same species or are so similar in their structure, life-cycles, and host-parasite relations as to be practically indistinguishable. This situation is particularly striking when the protozoa of monkeys are compared with those of other animals associated with man. If the proposition that close relationships of parasites indicate a common ancestry of their hosts is valid, then the facts available regarding the protozoan parasites of monkeys and man furnish evidence of importance in favor of the hypothesis that monkeys and man are of common descent.

LIST OF LITERATURE

ADLER, S. 1923. Malaria in chimpanzees in Sierra Leone. *Ann. Trop. Med. & Parasit.*, **17**: 13.

BACH, F. W. 1923. Zur Kenntnis der bei Affen vorkommenden Entamöben. *Arch. Schiffs. Trop. Hyg.*, **27**: 31–37.

BLACKLOCK, B. and ADLER, S. 1922. A parasite resembling *Plasmodium falciparum* in a chimpanzee. *Ann. Trop. Med. and Parasit.*, **16**: 99–106.

———. 1924. A malaria parasite of the chimpanzee. *Ann. Trop. Med. and Parasit.*, **18**: 1.

BOECK, W. C. and DRBOHLAV, J. 1925. The cultivation of *Endamoeba histolytica*. *Amer. Journ. Hyg.*, **5**: 371–407.

BRANCH, A. and GAY, D. M. 1927. Diarrhea in monkeys (*Macacus rhesus*) with oesophagostomum, strongloid and trichomonas infections. *Amer. Journ. Trop. Med.*, **7**: 97–110.

BROOKS, H. 1903. A few animal parasites sometimes found in man. *Proc. N. Y. Path. Soc.* (N. S.), **3**: 28.

BRUG, S. L. 1921. *Endolimax kueneni*, n. sp., parasitic in the intestinal tract of the monkey, *Macacus cynomolgus*. *Parasit.*, **12**: 378–379.

———. 1923. Protozoölogische Waarnemingen. *Geneesk. Tijdschr. Nederl.-Indië.*, **63**: 620–634.

BRUMPT, E. 1909a. Démonstration du rôle pathogène du *Balantidium coli*, etc. *C. R. Soc. Biol.*, **67**: 103.

———. 1909b. Remarks on entamoebae and *Trichomonas* in monkeys. *Bull. Soc. Path. Exot.*, **2**: 20.

BRUMPT, E. and JOYEUX, Ch. 1912. Sur un infusoire nouveau parasite du chimpanzé, *Troglodytella abrassarti*, n. g. n. sp. *Bull. Soc. Path. Exot.*, **5**: 499–503.

CASTELLANI, A. 1908. Note on a liver abscess of amoebic origin in a monkey. *Parasit.*, **1**: 101–102.

CHAGAS, C. 1918. (Host of *Trypanosoma cruzi*.) *Rev. Med. Cirurg.*, Brazil, **26**: 220.

———. 1924. Infection naturelle des singes du Para (*Crysotbrix sciureus* L.) par *Trypanosoma cruzi*. *C. R. Soc. Biol.*, **90**: 873.

CHRISTELLER, E. 1922. Ueber die Balantidienruhr bei den Schimpansen des Berliner Zoölogischen Gartens. *Virchow's Arch.*, **238**: 396–422.

CLEVELAND, L. R. 1926. Symbiosis among animals with special reference to termites and their intestinal flagellates. *Quart. Rev. Biol.*, **1**: 51–60.

CUNHA, A. M. DA and MUNIZ, J. 1927. Sobre os ciliados do genero *Balantidium* parasitos dos Macacos. *Boletim Biol.*, Fasc. **5**: 6–15.

DESCHIENS, R. 1926. *Chilomastix* sp. observé chez le chimpanzé, etc. *Bull. Soc. Path. Exot.*, **19**: 794–798.

———. 1927. Sur les protozoaires intestinaux des singes. *Bull. Soc. Path. Exot.*, **20**: 19–23.

DOBELL, C. 1926. (Amoebae of monkeys.) *Rept. Med. Res. Council*, **1924–25**: 31–33.

———. 1927. Further observations and experiments on the cultivation of *Entamoeba histolytica* from cysts. *Parasit.*, **19**: 288–313.

ELLIOT, D. G. 1913. A Review of the Primates. 3 vols. New York.

FONSECA, O. O. R. DA. 1915. Sobre os flagellados dos mammiferos do Brazil. Um novo parasito do homen. *Brazil-Medico.*, **29**: 281.

———. 1917. Sobre os flagellados parasites. *Brazil Medico.*, **31**: 417.

FORDE, R. M. 1902. Some clinical notes on a European patient in whose blood a trypanosome was observed. *Journ. Trop. Med. and Hyg.*, **5**: 261.

FRANCHINI, F. 1912. Experimentelle Tropendysenterie. Die *Entamoeba* beim Affen. *Centrlb. Bakt.*, **61**: 590–595.

GONDER, R. and GOSSLER, H. 1908. Untersuchungen über Malariaplasmodien der Affen. *Malaria*, **1**: 47.

GONDER, R. and RODENWALDT, E. 1910. Experimentelle Untersuchungen über Affenmalaria. *Centralbl. Bakt.* I Abt., **54**: 236–240.

GREIG, E. D. W. and WELLS, R. T. 1911. Dysentery and liver abscess in Bombay. *Sci. Mem. Med. and San. Dept. Gov. India.* **47**. 78 pp. Calcutta.

HALBERSTÄDTER, L. and PROWAZEK S. v. 1907. Untersuchungen über die Malariaparasiten der Affen. *Arb. K. Gesundheitsamte*, **26**: 37.

HEGNER, R. W. 1924. *Giardia* and *Chilomastix* from monkeys, *Giardia* from the wild cat and *Balantidium* from the sheep. *Journ. Parasit.*, **11**: 75–78.

———. 1926a. Host-parasite specificity among human protozoa. *Science Progress*, **21**: 249–259.

———. 1926b. The biology of host-parasite relationships among protozoa living in man. *Quart. Rev. Biol.*, **1**: 393–418.

———. 1926c. The transmission of human protozoa. *Sci.*, **64**: 28–34.

———. 1927. Host-Parasite Relations Between Man and His Intestinal Protozoa. 231 pp. New York.

———. 1928. Experimental transmission of trichomonads from the intestine and vagina of monkeys to the vagina of monkeys (*Macacus rhesus*). *Journ. Parasit.*, (In press).

HEGNER, R. W. and HOLMES, F. O. 1923. Observations on a *Balantidium* from a Brazilian monkey, *Cebus variegatus*, E. Goeffr., etc. *Amer. Journ. Hyg.*, **3**: 252–263.

HEGNER, R. W. and PAYNE, G. C. 1921. Surveys of intestinal protozoa of man, in health and disease. *Scientific Monthly*, **12**: 47–52.

HEGNER, R. W. and RATCLIFFE H. L. 1927. Trichomonads from the vagina of the monkey, mouth of cat and man, and intestine of monkey, opossum and prairie dog. *Journ. Parasit.*, **14**: 27–35.

HEGNER, R. W. and TALIAFERRO, W. H. 1924. Human Protozoōlogy. 597 pp. New York.

HINSHAW, H. C. 1926. Correlation of protozoan infections of human mouth with extent of certain lesions in pyorrhea alveolaris. *Proc. Soc. Exp. Biol. and Med.*, **24**: 71–73.

HOARE, C. A. 1925. Sections of the intestine of a kitten presumably infected with *Entamoeba histolytica* by rectal injection of cysts alone. *Trans. Roy. Soc. Trop. Med. and Hyg.*, **19**: 277–278.

HOGUE, M. J. 1926. Studies on *Trichomonas buccalis*. *Amer. Journ. Trop. Med.*, **6**: 75–88.

JHERING, H. v. 1902. Die Helminthen als Hilfsmittel der zoogeographischen Forschung. *Zool. Anzeig.*, **26**.

JOYEUX, C. 1913. Note sur quelques protozoaires sanguicoles et intestinaux observés en Guinée française. *Bull. Soc. Path. Exot.*, **6**: 612–615.

KESSEL, J. F. 1924. The experimental transfer of certain intestinal protozoa from man to monkeys. *Proc. Soc. Exp. Biol. and Med.*, **22**: 206–208.

———. 1926a. Some similarities between the dysentery amoeba of the monkey and of man. *Proc. Soc. Exp. Biol. and Med.*, **23**: 675–676.

KESSEL, J. F. 1926b. Trichomoniasis in kittens. *Proc. Soc. Exp. Biol. and Med.*, **24**: 200–202.

———. 1927. Intestinal protozoa of monkeys. *Journ. Parasit.*, **13**: 283–284.

KIKUTH, W. 1927. Piroplasmose bei Affen. *Arch. Schiffs. Trop. Hyg.*, **31**: 37–41.

KNOWLES, R. 1919. Notes on a monkey plasmodium and on some experiments in malaria. *Indian Journ. Med. Res.*, **7**: 195–202.

KOFOID, C. A. and SWEZY, O. 1921. On the free, encysted, and budding stages of *Councilmania lafleuri*, a parasitic amoeba of the human intestine. *Univ. Calif. Pub. Zoöl.*, **20**: 169–198.

KORKE, V. T. 1914. A note on the production of localized lesions by *Leishmania donovani* in *Macacus sinicus*. *Indian Journ. Med. Res.*, **I**, 622.

LANGERON, M. 1920. Sur une hémogrégarine d'une macaque. *Bull. Soc. Path. Exot.*, **13**: 165–167.

LAVERAN, A. 1880. Note sur un nouveau parasite trouvé dans le sang de plusieurs malades atteints de fièvre palustre. *Bull. Acad. Méd.*, **9**: 1235.

———. 1899. Les hématozoaires endoglobulaires (Haemocytozoa). *Cinq. d. l. Soc. Biol.*, Vol. jub., 124.

LEGER, A. 1922. Corps de Graham-Smith dans les hématies d'un primate (*Macacus rhesus*). *Bull. Soc. Path. Exot.*, **15**: 679–680.

LEGER, M. 1922. *Plasmodium* d'un singe de la Guinée française, *Cercopithecus campbelli* Wath. *C. R. Soc. Biol.*, **86**: 837.

LEGER, M. and BÉDIER, E. 1922. Hémogrégarine du cynocéphale, *Papio sphinx* E. Geoff. *C. R. Soc. Biol.*, **87**: 933.

LEGER, M. and BOUILLIEZ, M. 1912. Sur un *Plasmodium* des singes. *C. R. Soc. Biol.*, **73**: 310.

———. 1913. Recherches expérimentales sur *Plasmodium inui* Halberstädter et Prowazek d'un *Macacus cynomolgus*. *Ann. Inst. Pasteur*, **27**: 955.

LOESCH, F. 1875. Massenhafte Entwickelung von Amöben im Dickdarm. *Arch. Path. Anat.*, **65**: 196–211.

MACFIE, J. W. S. 1915. A case of dysentery in a monkey, in which amoebae and spirochaetes were found. *Ann. Trop. Med. Parasit.*, **9**: 507–512.

MATHIS, C. 1913. Entamibes des singes. *Bull. Soc. Med.-Chir. Indochine*, **4**: 388.

MAYER, M. 1908. Über Malariaparasiten bei Affen. *Arch. Protist.*, **12**: 314–321.

McCARRISON, R. 1919. The pathogenesis of deficiency disease. *Indian Journ. Med. Res.*, **7**: 283–345.

Mello, U. 1923. L'amebiasi nei primati. *Ann. d'Igiene.*, **33**: 533–552.

Mesnil, F. and Roubaud, E. 1917. Sur la sensibilité du chimpanzé au paludisme humain. *C. R. Acad. Sci.*, **165**: 39.

———. 1920. Essais d'inoculation du paludisme au chimpanzé. *Ann. Inst. Pasteur*, **34**: 466.

Metcalf, M. M. 1923. The opalinid ciliate infusorians. *U. S. Nat. Mus., Bull.* **120**: pp. 1–484.

Nicolle, C. and Sicre, A. 1908. Reproduction expérimentale du bouton d'orient chez le singe (*Macacus sinicus*). *C. R. Soc. Biol.*, **64**: 1096.

Noc, F. 1908. Un cas de dysenterie à *Balantidium* chez le *Macacus cynomolgus*. *C. R. Soc. Biol.*, **64**: 878–880.

Prowazek, S. v. 1912. Weiterer Beitrag zur Kenntnis der Entamöben. *Arch. Protist.*, **26**: 241–249.

Reichenow, E. 1917. Parasitos de la sangre y del intestino de los monos antropomorfos africanos. *Bol. R. Soc. Exp. de Historia Nat.*, **17**: 312.

———. 1920a. Den Wiederkäuer-Infusorien verwandte Formen aus Gorilla und Schimpanse. *Arch. Protist.*, **41**: 1–33.

———. 1920b. Ueber das Vorkommen der Malaria Parasiten des Menschen bei den Afrikanischen Menschenaffen. *Centrlb. Bakt. und Parasit.* Orig., **85**: 207–216.

Ross, P. H. 1905. A note on the natural occurrence of piroplasmosis in the monkey (*Cercopithecus*). *Journ. Hyg.*, **5**: 18–20.

Row, R. 1912. Some experimental facts *re* kala-azar (Indian). *Journ. Trop. Med. & Hyg.*, **15**: 327–328.

Scott, M. J. 1927. Studies on the balantidium from the guinea-pig. *Journ. Morph.*, **44**: 417–465.

Sluiter, C. P., Swellengrebel, N. H. and Ihle, J. E. W. 1922. De dierlijke parasieten van den mensch en van onze huisdieren. 3 edit., Amsterdam, 121 pp.

Smith, S. C. 1928. Host-parasite relations between *Iodamoeba williamsi* and certain mammalian hosts (guinea-pigs and rats). *Amer. Journ. Hyg.*, **8**: 1–15.

Stiles, C. W. and Orleman, M. B. 1927. The nomenclature for man, the chimpanzee, the orang-utan, and the barbary ape. *U. S. Hyg. Lab. Bull.* **145**: 66 pp.

Suldey, E. W. 1924. Dysenterie amibienne spontanée chez le chimpanzé (*Troglodytes niger*). *Bull. Soc. Path. Exot.*, **17**: 771–773.

Thézé, J. 1916. Pathologie de la Guyane française. *Bull. Soc. Path. Exot.*, **9**: 376–402, 449–469.

Tyzzer, E. E. and Walker, E. L. 1919. A comparative study of *Leishmania infantum* of infantile kala-azar and *Leptomonas* (*Herpetomonas*) *ctenocephali* parasitic in the gut of the dog flee. *Journ. Med. Res.*, **40**: 129–176.

Vogel, H. 1927. Über Kulturen der Ruhramöbe und deren Beinflussung durch Yatren. *Arch. Schiffs. Trop. Hyg.*, **31**: 74–88.

Walker, E. L. 1913. Experimental balantidiosis. *Phil. Journ. Sc.* (B), **8**: 333–349.

Wenyon, C. M. 1913. A further note on a case of dermal leishmaniasis from South America, with the results of inoculation experiments. *Journ. London Sch. Trop. Med.*, **2**: 117–119.

———. 1926. Protozoölogy. 2 vols. 1563 pp. London.

Ziemann, H. 1925. Einige Bemerkungen zur *Balantidium-coli*-Infektion bei Menschen und Schimpansen. *Beih. Arch. Schiffs. Trop. Hyg.*, **29**: 434–448.

HALDANE ON SELECTION

By LOWELL J. REED

School of Hygiene and Public Health, Johns Hopkins University

(*Paper No. 141 from The Department of Biometry and Vital Statistics*)

THE modern theories of inheritance are sufficiently definite to tempt the mathematically inclined to subject them to analysis for the sake of determining the consequences that flow from them. Pearson (1), Warren (2), Norton (3), and Jennings (4) have dealt with certain phases of the problem, but by far the most thoroughgoing treatment has been given in a series of papers by J. B. S. Haldane (5). The present article is a review of the method of approach and the results obtained in this excellent series of papers.

The author has defined the general problem by stating that when given (1) the mode of inheritance of the character considered, (2) the system of breeding in the group of organisms studied, (3) the intensity of selection, (4) its incidence (that is, on both sexes or only one), it should be possible to state the value of (5) the rate at which the proportion of organisms showing the character increases or diminishes, in terms of (3) the intensity of selection. Conditions (1), (2), and (4) define the problem as to its position in the general theory of inheritance, and (3) and (5) are the variables whose interrelationship we wish to determine within the universe defined by (1), (2), and (4). To formulate the problem mathematically, the author defines intensity of selection by the statement that "if a generation of zygotes immediately after fertilization consists of two phenotypes A and B in the ratio $pA{:}1B$, and the proportion which forms a fertile union is $pA{:}(1\text{-}k)B$, we shall describe k as the coefficient of selection". This index k is used by the author to measure the intensity of selection, and it may take values between 1 and $-\infty$. At the extremes selection is complete, for when $k = 1$, no B's reproduce and when $k = -\infty$, no A's reproduce. When k is small, selection is slow; if k is positive, it is in favor of the A's and if negative, in favor of the B's.

If the nth generation consists of types A and B in the ratio $u_n\ A{:}1B$ $\left(\text{or if the proportion of } B\text{'s in the total universe is } y_n \text{ where } y_n = \frac{1}{1 + u_n}\right)$, the problem resolves itself into the determination of the functional relationship between u_n (or y_n) and k, under different modes of inheritance and different systems of breeding.

All of the papers of this series are concerned with the determination of such functional relationships under a wide variety of conditions, and the consideration of some of the general conclusions that follow from such an analysis.

The first paper deals with some of the

different cases that arise when selection of small and constant intensity operates on Mendelian populations where generations do not overlap either during random mating or when all zygotes are self-fertilized. The cases considered and their results are as follows:

CASE A: SELECTION IN THE ABSENCE OF AMPHIMIXIS

The simplest form of selection is uncomplicated by amphimixis and is illustrated in the following cases:

1. Organisms which do not reproduce sexually, or are self-fertilizing.
2. Species which do not cross, but compete for the same means of support.
3. Organisms in which mating is always between brother and sister.
4. Organisms which are haploid during part of the life cycle, provided that the selection of the character considered occurs only during the haploid phase.
5. Heterogamous organisms in which the factor determining the character selected occurs in the gametes of one sex only.

Setting up the functional relationship between y_n and k for this type of selection, the author finds that $y_n = \frac{1}{1 + (1-k)^{-n}}$, when the initial conditions are such that the number of A's equals the number of B's. For small values of k, that is, when selection is slow, this formula becomes approximately $y_n = \frac{1}{1 + e^{kn}}$, the logistic reaction. For this condition, we see that the proportion of B's falls slowly for a time, then more rapidly, and then slowly again, the most rapid change in the proportion occurring when the number of B's is equal to the number of A's, that is, when $y_n = \frac{1}{2}$. For this mode of inheritance, selection proceeds more rapidly than for any of the other systems of inheritance considered. The speed must compensate to some extent for the failure to combine advantageous factors by amphimixis.

CASE B: SELECTION OF A SIMPLE MENDELIAN CHARACTER

This is the mode of inheritance that has been subjected to mathematical analysis more often than any other. Pearson (6) and Hardy (7) have shown that in the case of random mating, the number of heterozygotes is equal to four times the product of the numbers of the two homozygous classes. Thus, if $u_nA:1a$ be the proportion of the two types of gametes produced in the $(n-1)^{th}$ generation, then in the nth generation the initial proportions of the three classes of zygotes are $u_n^2AA:2u_nAa:1aa$. The proportion of recessives to the whole population is $y_n = (1 + u_n)^{-2}$. Now, only $1-k$ of the recessives survive to breed, so that the survivors are in the proportion $u_n^2AA:2u_nAa:(1-k)aa$. This leads to an expression for u_{n+1} in terms of u_n and k as follows: $u_{n+1} = \frac{u_n(1 + u_n)}{1 + u_n - k}$. It can be easily shown that this result follows from random mating. If, now, we know the original proportion of recessives, and we start with a population $u_0^2AA:2u_0Aa:1aa$, where $u_0 = y_0^{-1/2} - 1$, we can at once obtain u_1 by use of the equation $u_1 = \frac{u_0(1 + u_0)}{1 + u_0 - k}$, and by use of this recurring formula, we can determine u_n and therefore y_n.

If the selection is complete,—that is, if all of the dominants are killed off or prevented from breeding,—the case becomes very simple, and y_n is equal to unity.

If, on the other hand, all the recessives die, k becomes equal to 1 and the above general equation reduces to $y_n = y_0(1 + ny_0^{1/2})^{-2}$. This equation shows that

999 generations would be needed to reduce the proportion to one in one million, and we need not therefore be surprised that recessive sports still occur in most of our domestic breeds of animals.

For the case where selection is not very intense, the author has simplified the general recurring equation to the form $kn = u_n - u_0 + \log_e \frac{u_n}{u_0}$. Then starting from or working toward a standard population containing 25 per cent recessives, for which $u_0 = 1$, we have $kn = u_n + \log_e u_n - 1$. This equation gives to a sufficiently exact degree of approximation the relationship between n the number of generations, k the intensity of selection, and u_n. Since making k negative gives the effect of a selection that favors the recessives at the expense of the dominants, we can use this equation and the equation $y_n = (1 + u_n)^{-2}$ to compute for different values of kn the proportion of recessives when either dominants or recessives are favored. This the author has done in Table I, so that we may use this table to run forward and backward from a standard population of 75 per cent dominants and 25 per cent recessives, and determine the change in the per cent of recessives for any number of generations.

Table 2 has been set up from the same equation except that values of kn are tabulated against the percentages of the favored type. These two tables are very convenient for the actual examples in selection.

TABLE 1

Effect of slow selection on an autosomal Mendelian character

kn (number of generations × k)	Per cent of recessives when dominants are favored	Per cent of recessives when recessives are favored
−1000		0.0001
−100		0.0105
−50		0.0427
−20		0.2773
−15	99.9998	0.4215
−10	99.975	1.036
−9	99.933	1.254
−8	99.82	1.545
−7	99.50	1.940
−6	98.68	2.497
−5	96.50	3.308
−4.5	94.38	
−4	91.14	4.537
−3.5	86.36	
−3	79.71	6.528
−2.5	71.24	
−2	61.53	9.718
−1.5	50.68	12.11
−1	40.98	15.30
−0.5	32.05	19.53
0	25.0	25.0
0.5	19.53	32.05
1	15.30	40.98
1.5	12.11	50.68
2	9.718	61.53
2.5		71.24
3	6.528	79.71
3.5		86.36
4	4.537	91.14
4.5		94.38
5	3.308	96.50
6	2.497	98.68
7	1.940	99.50
8	1.545	99.82
9	1.254	99.933
10	1.036	99.975
15	0.4215	99.9998
20	0.2773	
50	0.0427	
100	0.0105	
1000	0.0001	

CASE C: FAMILIAL SELECTION OF A SIMPLE MENDELIAN CHARACTER

This is a case of a factor A, whose presence gives an embryo possessing it an advantage measured by k over those members of the same family which do not possess it. For this case the law used in the preceding section does not hold.

If the family has both parents in common, as in mammals, and we let the population consist of $p_n AA : 2q_n Aa : r_n aa$, where $p_n + 2q_n + r_n =$ unity, then in a

mixed family where equality would have been expected, the ratio of dominants to recessives will be $1:1-k$. For the case where k is small, we can let $u_n = \frac{p_n + q_n}{q_n + r_n}$, and arrive at the following relationship: $u_{n+1} = u_n + \frac{ku_n}{2(1 + u_n)}$, which in turn may be simplified to give a relationship between u_n and k as follows: $1/2kn = u_n + \log_e u_n - 1$. A comparison of this last relationship with the one derived for selection of a simple Mendelian character shows that the species changes its composition at one-half the rate at which it would change if selection worked on the species as a whole, and not within families only.

If the family has the mother only in common, but fathers are a random sample of the population, as in the case in cross-pollinating seed plants, we find a relationship of the type $3/4kn = u_n + \log_e u_n - 1$ for the case where k is small. Thus selection proceeds at three-quarters of the rate which exists in the case of a selection of a simple Mendelian character.

CASE D: SEX-LIMITED CHARACTERS AND UNISEXUAL SELECTION

When the characters appear in only one sex, as in the case with milk-yield or other secondary sexual characters, we may let the $n-1$ generation form spermatozoa in the ratio $u_nA:1a$, and eggs in the ratio $v_nA:1a$, in which case the nth generation consists of zygotes in the ratio $u_nv_nAA:(u_n + v_n)\,Aa:1aa$. In this case, $y_n = (1 + u_n)^{-1}\,(1 + v_n)^{-1}$. With complete selection, when $k = -\infty$, this case reduces to $y_n = 1 + 2^{1-n}\,(y_0^{1/2} - 1)$, where the proportion of dominants is halved in every successive generation. When $k = 1$, and all the recessives of one sex die childless, the proportion of recessives in successive generations, starting from the standard populations, is 25 per cent, 16.7 per cent, 12.5 per cent, 9.56 per cent, 7.94 per cent, etc. When the rate of selection is slow,—that is, k is small,—our equation becomes $1/2kn = u_n + \log_e u_n - 1$, which shows that selection proceeds at one-half the rate for slow selection of a simple Mendelian character.

TABLE 2

Effect of slow selection on an autosomal Mendelian character

Per cent of favored type					0.0001	0.001	0.01	0.05
kn when dominants are favored					−15.51	−13.21	−10.90	−9.294
kn when recessives are favored					−1005.0	−320.0	−102.60	−45.50
0.1	0.2	0.5	1	2	3	5	10	15
−8.600	−7.905	−6.996	−6.286	−5.580	−5.161	−4.624	−3.863	−3.290
−33.04	−23.42	−14.72	−10.197	−6.875	−4.976	−3.717	−1.933	−1.041
20	25	30	35	40	45	50	55	60
−2.979	−2.712	−2.439	−2.180	−1.964	−1.708	−1.467	−1.220	−0.962
−0.448	0	+0.366	+0.681	+0.962	+1.220	+1.467	+1.708	+1.964
65	70	75	80	85	90	95	97	98
−0.681	−0.366	0	+0.448	+1.041	+1.933	+3.717	+4.976	+6.875
+2.180	+2.439	+2.712	+2.979	+3.290	+3.863	+4.620	+5.161	+5.580
99	99.5	99.8	99.9	99.95	99.99	99.999	99.9999	
+10.197	+14.72	+23.42	+33.04	+45.50	+102.60	+320.0	+1005.0	
+6.286	+6.996	+7.905	+8.600	+9.294	+10.90	+13.21	+15.51	

This result was previously given by Punnett (8).

CASE E: SELECTION OF AN ALTERNATIVELY DOMINANT CHARACTER

Certain factors, such as those determining the presence or absence of horns in Dorset and Suffolk sheep according to Wood (9), are dominant in one sex and recessive in the other. With complete selection, all members of the type dominant in the female sex are weeded out. With $k = 1$, the type disappears in the male sex and is halved in successive female generations. If $k = -\infty$, the recessive type in the female sex disappears in that sex and is halved in successive male generations. For small values of k, that is, for a low rate of selection, we have $kn = 2\log_e u_n$, so that selection occurs on the whole more rapidly than in the case of a simple Mendelian character.

CASE F: BISEXUAL SELECTION OF A SEX-LINKED CHARACTER

The case of selection in a population whose members differ with regard to a sex-linked factor leads to the conclusion that for complete selection, no dominants survive to breed and the selection is complete in one generation. If $k = 1$, and no recessives survive to breed, there are no recessive females produced and the number of recessive males is halved in each generation. Selection is therefore vastly more effective than on an autosomal character. If colorblind or hemophilic people were prevented from breeding, these conditions would be almost abolished in a few generations, which would not be the case with feeble-mindedness.

In the case of slow selection, if generations are reckoned from a standard population when $u_0 = 1$, and 50 per cent of the males and 25 per cent of the females are recessives, we find that within an error of the order of k, we have

$$kn = \log_e u_n + 2\log\left(\frac{3 + u_n}{4}\right)$$

and

$$y_n = (1 - u_n)^{-2}$$

$$z_n = (1 + u_n)^{-1}$$

when y_n = per cent of recessives of the homozygous sex and z_n = per cent of recessives of the heterozygous sex. Thus selection acts more rapidly on a sex-linked character in the homozygous sex than on an autosomal character and at about the same rate in the heterozygous sex as on an autosomal character.

CASE G: BISEXUAL FAMILY SELECTION OF A SEX-LINKED CHARACTER

Considering the case where the family within which selection occurs has both parents in common and letting the dominants have an advantage of 1 to $1 - k$ over the recessives in the mixed families, the author finds that with complete selection for $k = 1$ the recessives disappear at a very fast rate. When k is small, the selection proceeds more as in the case of racial selection, but at from one-half to one-third of the rate.

CASE H: SELECTION OF A SEX-LINKED CHARACTER IN THE HOMOZYGOUS SEX ONLY

Several sex-linked factors are known which have a much more marked effect on the homozygous than the heterozygous sex; thus in *Drosophila melanogaster* "fused" females are sterile, males are fertile, while the character "dot" occurs in 8 per cent of the genetically recessive females, but only 0.8 per cent of the males (Morgan and Bridges, 10). Under these conditions, with complete selection for $k = -\infty$, the dominants disappear in two generations.

If $k = 1$, the elimination is vastly slower than when selection occurs in both sexes. If k is small, the selection of the homozygotes proceeds as in the case of slow selection on an autosomal Mendelian character, while the heterozygous sex changes rather more slowly.

CASE I: SELECTION OF A SEX-LINKED CHARACTER IN THE HETEROZYGOUS SEX ONLY

In certain cases, sex-linked factors appear only or mainly in the heterozygous sex. For example, in *Drosophila melanogaster* "eosin" eye-color is far more marked in the male than in the female, and the sex-linked fertility factor L_2 postulated by Pearl (11) in poultry can show only in the female sex. Under these conditions we find that for complete selection, $k = -\infty$, the number of dominants is halved in each generation after the second. If the recessives are eliminated and $k = 1$, the proportion of recessives is halved in each generation. If the selection is slow, $kn = 3 \log u_n$ and the selection of the heterozygous sex proceeds along the logistic curve but at one-third the rate of an autosomal Mendelian character, while the selection in the homozygous sex is slightly faster.

CASE J: CERTATION, OR GAMETIC SELECTION OF AN AUTOSOMAL CHARACTER

Gametes or gametophytes may be selected according to what factors they carry, and while such selection may be wide, it is more likely to be among the gametes of the same individual. Considering the gametes of one gender to be affected by selection, we find that for complete selection if all the dominant-carrying gametes are eliminated, $k = -\infty$, the proportion of dominants is halved in each generation. If all recessive carriers are eliminated, no recessive zygotes appear and the proportion of heterozygotes is halved in each generation. If selection is slow,

$$kn = 2 \log_e u_n$$

and

$$y_n = (1 + u_n)^{-2}$$

A comparison of the results of complete selection for the more important cases is given in Table 3. Selection is supposed to begin on a population in equilibrium, containing equal numbers of dominants and recessives of the sex considered. The author comments on this table as follows: "It is worth noting that in the case of sex-linked characters, and autosomal recessives when selection is gametic, individuals of types which have wholly disappeared reappear if selection ceases. With many types of heredity dominants are eliminated in one or two generations, and where this is not the case they generally decrease more rapidly than recessives."

The rate of slow selection has been determined less rigorously than in the case of rapid selection, but the effect of the approximation is slight. Table 4 shows the effect of slow selection in the various cases considered, the rate of selection in this case being one in a thousand, that is, a thousand of the type considered survive for every 999 of the other.

A consideration of all of the cases dealt with in this paper shows that selection is most rapid when amphimixis is avoided by one means or another. Moreover, selection is ineffective on recessive characters when these are rare, except in the case of sex-linked factors, when it is effective in the homozygous sex and in gametic selection. It seems, therefore, very doubtful whether natural selection in random mating organisms can cause the spread of autosomal recessive

characters unless they are extraordinarily valuable to their possessors. Such characters appear far more frequently than dominant mutations, but in their early states are selected infinitely more slowly.

In Part II (5) of this series of papers, the author considers the influence of partial self-fertilization, inbreeding, assortative mating, and selective fertilization on the composition of Mendelian populations and on natural selection, and finds that for partial self-fertilization and partial inbreeding, the selection is rapid when the recessives are few. Partial assortative mating and selective fertilization on the other hand have but slight effect on the rapidity of selection. The case of inbreeding is of importance since the moderate degree of inbreeding which must occur in human populations in such instances as the mating of cousins will enormously increase the number of recessives when these recessives are sufficiently rare. Assortative mating, which has been shown by Pearson (12) to exist in human populations, will on the other hand have but little effect. Hence, inbreeding or self-fertilization appears to be necessary in early stages of selection of a recessive character if this process is to be fast enough to be an effective cause of evolution. Inbreeding and self-fertilization cannot be replaced by moderate degrees of selective mating or fertilization.

TABLE 3

Effects of complete selection

CHARACTER ELIMINATED	TYPE OF SELECTION	SEX	PER CENT AFTER 5 GENERATIONS FROM 50 PER CENT	PER CENT AFTER 10 GENERATIONS FROM 50 PER CENT
Non-amphimictic	Any	Both	0	0
Autosomal dominant	Bisexual	Both	0	0
Autosomal recessive	Bisexual	Both	2.44	0.768
Autosomal dominant	Unisexual	Both	1.83	0.0572
Autosomal recessive	Unisexual	Both	8.88	3.27
Sex-linked dominant	Bisexual	Homozygous	0	0
		Heterozygous	0	0
Sex-linked recessive	Bisexual	Homozygous	0	0
		Heterozygous	1.56	0.0484
Sex-linked dominant	In homozygous sex	Homozygous	0	0
		Heterozygous	0	0
Sex-linked recessive	In homozygous sex	Homozygous	5.34	1.74
		Heterozygous	18.5	13.28
Sex-linked dominant	In heterozygous sex	Homozygous	1.83	0.0572
		Heterozygous	3.125	0.0977
Sex-linked recessive	In heterozygous sex	Homozygous	0	0
		Heterozygous	3.125	0.0977
Autosomal dominant	Gametic unisexual	Both	1.83	0.0572
Autosomal recessive	Gametic unisexual	Both	0	0

In Part III (5), the author considers the cases of a single but completely dominant factor and of several interacting factors. Mating is supposed to be at random, the populations to be very large, and the generations not to overlap. He derives for these cases expressions for the changes caused by slow selection in

populations whose characters are determined by incompletely dominant, multiple or polyploid factors, and for the equilibria attained in certain of the cases. For a multiple autosomal recessive character, selection is shown to be lower than in the case of a character determined by one factor alone, although when the dominants are very rare or when one of the multiple factors greatly outweighs the rest, it proceeds at about the same rate in the two cases. Selection is slowest for the multiple case when the factors are of equal weight. Similar results are obtained in the cases of multiple sex-linked recessive characters and multiple autosomal dominant characters, selection being slower in the multiple case.

For the case of linkage between the autosomal factors, the proportions of the various types of gametes are shown to approach asymptotically those which would be reached in one generation without linkage.

TABLE 4

Generations required for a given change with various types of slow selection

$k = 0.001$

DOMINANT FACTOR FAVORED	TYPE OF SELECTION	SEX	CHANGE IN PERCENTAGE			
			0.001–1	1–50	50–99	99–99.999
Non-amphimictic	Bisexual racial	Both	6,921	4,592	4,592	6,921
Autosomal	Bisexual racial	Both	6,920	4,819	11,664	309,780
Autosomal	Unisexual racial / Bisexual familial	Both	13,841	9,638	23,328	619,560
Autosomal	Bisexual familial†	Both	9,227	6,425	15,522	413,040
Autosomal*	Bisexual racial	♂	13,831	8,819	6,157	7,112
Sex-linked	Bisexual racial	Homozygous	6,916	4,668	5,593	10,106
		Heterozygous	6,928	5,164	11,070	20,693
Sex-linked	Bisexual familial	Homozygous	20,753	13,785	13,785	20,753
		Heterozygous	20,768	14,987	24,332	41,450
Sex-linked	Racial of homozygous sex	Homozygous	10,380	7,228	17,496	464,670
		Heterozygous	10,392	8,378	153,893	149,860,377
Sex-linked	Racial of heterozygous sex	Homozygous	20,746	13,228	9,236	10,668
		Heterozygous	20,753	13,785	13,785	20,753
Autosomal	Unisexual gametic	Both	13,831	8,819	6,157	7,112
Autosomal	Unisexual gametic‡	Both	27,661	17,638	12,314	14,224
Sex-linked	Gametic of homozygous sex	Homozygous	10,373	6,619	4,618	5,334
		Heterozygous	10,377	6,892	6,892	10,377
Sex-linked	Gametic of homozygous sex‡	Homozygous	20,746	13,228	9,236	10,668
		Heterozygous	20,753	13,785	13,785	20,753

* Dominant in ♂, recessive in ♀.

† The families have only one parent in common.

‡ In heterozygous individuals gametes are replaced (as zygotes in familial selection).

The effect of selection on recessive characters may be found by inverting the order of the four numerical columns. Thus 309,780 generations are needed for an autosomal recessive to increase from 0.001 per cent to 1 per cent, 11,664 generations to increase from 1 per cent to 50 per cent, and so on.

Part IV (5) deals with the question of overlapping generations, and in it the author first takes up and demonstrates the theorem previously given by Lotka (13)

as to the stability of normal age distribution. Consideration of the effect of generations that overlap to the extent that they do in mankind shows that the changes due to slow selection are very similar to those which occur when generations are separate.

The last paper of the series, Part V (5), considers the subject of mutation. The frequency of occurrence of mutations is generally small, and on the whole, mutants recessive to the normal type occur more commonly than dominants. A consideration of selection in this case shows that if it acts against mutation it is ineffective, provided that the rate of mutation is greater than the coefficient of selection. Moreover, mutation is quite effective where selection is not: namely, in causing an increase of recessives where these are rare. It is also more effective than selection in weeding out rare recessives, provided it is not balanced by back-mutation of dominants. Mutation, therefore, determines the course of evolution as regards factors of negligible advantage or disadvantage to the species, but it can lead to results of importance only when its frequency becomes large.

This series of papers is not only valuable for the large number of cases treated, but it is extremely fertile in suggestions for possible extensions of the analysis. As it stands, it constitutes the most complete mathematical treatment of the effect of natural and artificial selection which has appeared.

LIST OF LITERATURE

(1) Pearson, K. 1896. Contributions to the mathematical theory of evolution. Note on reproductive selection. Proc. Roy. Soc., 59: 301–305.

(2) Warren, H. C. 1917. Numerical effects of natural selection acting upon Mendelian characters. Genetics, 2: 305–312.

(3) Norton, H. T. J. Work quoted by Punnett. See 8.

(4) Jennings, H. S. 1916–17. The numerical results of diverse systems of breeding. Genetics, 1: 53–89; 2: 97–154.

(5) Haldane, J. B. S. 1924–27. A mathematical theory of natural and artificial selection. Part I. Trans. Cambridge Phil. Soc., 23: 19–41. Part II. Proc. Cambridge Phil. Soc. (Biol. Sci.), 1: 158–163. Part III. Proc. Cambridge Phil. Soc., 23: 363–372. Part IV. *Ibid.*, 607–615. Part V. *Ibid.*, 838–844.

(6) Pearson, K. 1904. Mathematical contributions to the theory of evolution. XII. On a generalized theory of alternative inheritance, with special reference to Mendel's laws. Phil. Trans. Roy. Soc. A, 203: 53–86.

(7) Hardy, G. H. 1908. Mendelian proportions in a mixed population. Science N. S., 28: 49–50.

(8) Punnett, R. C. 1915. Mimicry in Butterflies. Cambridge University Press. vi + 188 pp. 16 plates.

(9) Wood, T. B. 1905. Note on the inheritance of horns and face colour in sheep. Journ. Agric. Science, 1: 364–365.

(10) Morgan, T. H., and Bridges, C. B. 1916. Sex-linked inheritance in *Drosophila*. Carnegie Inst. Wash. Publ. 237. 87 pp. 2 plates.

(11) Pearl, R. 1912. The Mendelian inheritance of fecundity in the domestic fowl. Amer. Nat., 46: 697–711.

(12) Pearson, K., and Lee, A. 1903. On the laws of inheritance in man. I. Inheritance of physical characters. Biometrika, 2: 357–462.

(13) Lotka, A. J. 1922. The stability of the normal age distribution. Proc. Nat. Acad. Sci., 8: 339–345.

SEASONAL MODIFICATIONS IN TESTES OF VERTEBRATES

By R. M. OSLUND

University of Illinois

THERE is an obvious relationship between the phenomena of sexual urge and of testicular activity. That the testis augments the mating instinct has long been known, and the literature contains a great deal of controversy concerning which of the testicular elements wields this influence.

In most animals there are seasonal variations in the size of the testis and in the relative quantity of its constituent elements. These changes are found in all animals that mate but once each year. In hibernating animals the changes appear to be more pronounced than in the non-hibernating forms. Where the seasonal changes in sexual behavior and in testicular structure are marked it is reasonable to expect that any parallelism between testicular modification and physiological action might be seen. Such a parallelism might be found between sex activity and (1) volume of a particular tissue or (2) cell proliferation or (3) cytological appearance. Each of these parallelisms has been reported as existing.

It has been difficult to ascertain the importance of any change in any of the tissue substances of the testis, partly because of the scarcity of studied material. This is true because most of the reports found in the literature are based upon observations covering only a few months of the year. A second difficulty has been due to the fact that in many reports the exact time of mating has not been noted. The failure to take into consideration the exact time of breeding rather than the approximate time of the year has caused much of the confusion and difference of opinions. Perhaps the greatest difficulty in studying the physiology of the testis has been caused by the fact that some writers have attempted to prove a theory with their facts instead of forming a theory to explain the observed facts. As a result, the literature contains many contradictory statements that are difficult to interpret.

In this review an attempt has been made to glean the facts from the literature upon seasonal changes in vertebrate testes and to present these facts in as clear a manner as possible. In order to do this the literature on the seasonal changes in each group of animals is reviewed separately and an attempt is made to evaluate these observations. The recorded observations are then discussed and interpreted with reference to the known facts regarding the time and peculiarities of sexual activities of these animals.

MODIFICATIONS IN THE TESTES OF FISH

Fish testes are made up of lobules containing cysts of germ cells. These lobules correspond to the spermatogenic tubules of mammals and empty into longitudinal collecting ducts which in turn open into

the epididymis and vas deferens. During the non-spermatogenic season these lobules are small and contain only a few germ cells. All cells in any one lobule are of one stage of development, the testis in this respect resembling that of arthropoda. As spermatogenesis progresses these lobules become filled with germ cells, and as the number and size of the cells increase the lobules become enlarged. This continues during multiplication and growth of spermatogonia and spermatocytes and perhaps during the early part of the spermatid period. Thereafter the size of the individual cells decreases without any augmentation in their number and the lobules thereupon decrease in size proportionately. When the sperm are ejected the lobules are emptied and suddenly decrease in volume.

Between the lobules are found connective tissue, blood and lymph vessels, and nerves. When the lobules are distended with spermatogenic tissue they press tightly against each other. The cells of the connective tissue lying between them then resemble typical connective tissue cells. When the lobules decrease in volume, during the spermatid and spermatozoa stages and especially when the spermatozoa are ejected, some of the connective tissue cells enlarge and become somewhat modified in structure. These cells are commonly referred to as interstitial cells and some authors maintain that they are glandular cells.

The entire mass of tissue between the lobules in fishes and amphibia and the tissue between the tubules in birds and mammals should be designated *intertubular tissue*, while the term *interstitial tissue* should include only the modified connective tissue cells. This distinction is necessary since an increase in the space between the tubules, *intertubular space*, does not always imply an increase in interstitial tissue. In a review of the literature this distinction is difficult to maintain since most writers have failed to note the differences, but the fact should not be overlooked in evaluating the reports.

Size of the testis in fish largely depends upon the size of the lobules. When the lobules enlarge the testis increases in volume. When the lobules shrink following sperm ejection the testicular volume does not proportionately decrease because of change in intertubular tissue, especially because of the interstitial cell increase in the case of fishes. Later, as the interstitial cells decrease in quantity, the testis further shrinks in volume.

Temperature of the water, abundance of food, and to some extent the amount of light are prime factors in the life of the fish. Anatomic and physiological seasonal modifications are especially influenced by changes in temperature. For example, if a female about to deposit her eggs is placed in very cold water, egg deposition may be delayed indefinitely.

In Yellow Perch (*Perca flavesans*) Turner (36) reports that the volume of the testis is greatest during late November. He also states that the maximum size is in January. His data indicate that the greatest weight is in November. The volume increase at this time is very rapid because of the increase in the number of germ cells in the lobules. The large size of the testis persists until early March and then suddenly falls when spawning takes place due to ejection of ripe sperm. This decrease continues from early March to late May. The beginning of increase in volume precedes the decline in temperature and is due to the early stages of spermatogenesis. The first spermatozoa are formed in the early part of September and are present in the lobules until their expulsion takes place the following spring. No data were given concerning the intertubular tissue.

Seasonal variations in the size of the

testis of the Top Minnow (*Gambusia affinis*) may be eightfold (18). The period of maximum size is from November to February. No spermatogenesis occurs during cold weather. Again no mention is made regarding interstitial cells. This should not be construed as indicating that they do not exist. The data offered by these two investigators show the relation between testicular size and spermatogenesis. This is in turn directly related to sex activity.

Courrier (12 and 13) reported that in the Stickleback (*Gasterosteus aculeatus*) spermatogenesis occurs during March. It progresses rapidly, so that by the end of the month it is completed and most of the lobules contain spermatozoa.

During spermatogenesis the seminal elements distend the cysts so that they press tightly against each other. Only a thin layer of connective tissue in addition to the blood vessels and nerves then separates the lobules. Courrier records that early in April after the end of spermatogenesis the interlobular spaces begin to change and that in May and June the cells in these spaces are filled with many mitochondria and secretion granules. He refers to these cells as forming an interstitial gland and suggests that they have increased because there exists a need for a product they secrete. According to Courrier, the purpose of these "glandular" cells is to secrete a testicular hormone which produces the bright, nuptial coloration and sex activity. He further states that in May and June fish that do not have the nuptial appearance have no trace of interstitial cells though they have spermatocytes and spermatogonia. These are probably males that mated early and have lost their mating apparel.

Champy (10) found many Sticklebacks with nuptial apparel in the winter but with interstitial cells poorly developed or absent. They are rare or absent at the time that spermatozoa ripen, which is at the opening of the mating season. He studied development in many other species of fish and could find no correlation between presence of interstitial cells and development of secondary sex characters or modifications of appearance that are found during the mating season. In *Spinachia vulgaris*, *Tinca vulgaris*, and *Phoxinus laevis* he found no trace of interstitial cells at any period of the year, yet males of these species develop sex characteristics and mating apparel. He found that these anatomic changes appeared to be correlated with the maturity of spermatozoa.

Van Oordt (37 and 38) also made observations upon *Gasterosteus aculeatus*. He found that the testicle at mating, the exact time of which he fails to designate, contains no spermatocytes but that it is then filled with spermatozoa. Large groups of interstitial cells are then found at the corners of two or three canals. In August, when secondary sex characters are largely gone and the tubules contain early stages of spermatogenesis, the intertubular spaces are quite wide and contain groups of interstitial cells. In October spermatogenesis has continued, distending the lobules, and only a few interstitial cells are then present (38). In winter, when secondary sex characters are not developed, he found some testes in which there existed a broad interstitium with many interstitial cells. In spring he found that secondary sex characters appear as spermatogenesis advances. He concludes from cytological findings that the interstitial cells increase when spermatogenesis is suspended because they become charged with nourishment. This stored up food is later consumed by developing germinal epithelium during the period of cell proliferation.

From the above data it is almost impossible to arrive at any positive conclusions regarding cytological changes throughout the year. Though Courrier, Champy, and Van Oordt made observations on the same species, *Gasterosteus aculeatus*, the data offered are very meager and do not cover the entire year. Much interpolation is necessary. Chart I, which is based on all available data, makes it quite certain that the interstitial cells do not promote the appearance of nuptial apparel in this species. These cells develop after maturity of spermatozoa. They increase as the mating season closes and are most abundant during the summer months, when the testes contain no sperm. When spermatogenesis again takes place they decrease. They follow rather than precede mating and are abundant in the testis when the tubules are empty. The latter fact has been emphasized by Van Oordt, who concludes from this relationship and from the cytological changes taking place in the interstitial cells that they are trophic cells. He maintains that they are abundant when the fatty material they contain is not being consumed by developing germinal cells.

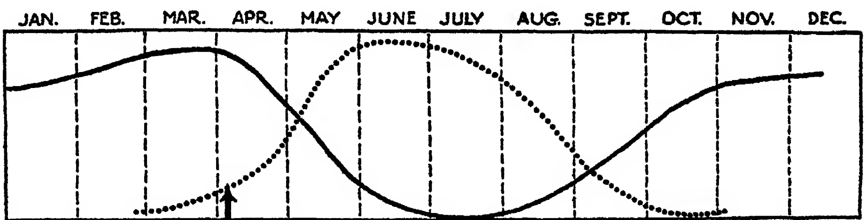


CHART I GASTEROSTEUS ACULEATUS

——— QUANTITY OF SPERMATIC TISSUE, ········ QUANTITY OF INTERSTITIAL TISSUE ↑ = MATING

MODIFICATIONS IN TESTES OF AMPHIBIA

The structure of the amphibian testis somewhat resembles that of the fishes. The spermatogenic cells are found in cysts and lobules, the latter being separated by intertubular tissue. Under certain conditions some of the intertubular connective tissue cells become modified into interstitial cells.

Anura generally breed in the spring, and their eggs may be seen in ponds or along the stream banks during high water of early spring. Urodeles, however, breed largely during midsummer and early fall. Some *may* breed in spring. With each species care must therefore be taken to note the cytological modifications of the testis and the anatomic and physiologic peculiarities with reference to the actual time of mating rather than to calendar month or seasonal period of the year. In most species spermatogenesis takes place in the summer immediately after mating and the spermatozoa are retained in the testis and spermatic passages during the winter.

Friedman (15) found tubuli of *Rana fusca*—now *Pelobates fuscus*—well filled with spermatogonia at the end of March, through April and May, and even in June. The tubules are angular in outline at that time from being pressed tightly together. There is little room for intertubular substance, and only blood vessels and connective tissue cells are present between the tubules. Toward the end of June, with spermatogenic progress, interstitial cells appear. In the fall, when all stages of spermatogenesis are found, the intertubular spaces are richly filled with interstitial

cells. At the end of October and during the winter months, when no spermatogenesis is going on (only spermatogonia are found), the interstitial cells disappear.

He does not indicate when mating occurs, merely stating that spermatogenesis is going on during the summer and that at the end of October only spermatogonia are present. From this it might be inferred that mating is in October when the products of the summer and fall wave disappear. From other sources of information it seems that the mating period is from the middle of March to the middle of May. Friedman was apparently observing the early stages of a wave of spermatogenesis whose products are kept until the following spring, as is true for other Amphibia.

Nor does he record the size of the tubules during spermatogenesis, though from his discussion of the early spring and late fall and winter conditions it appears that from June to September the tubules are not distended but round and the intertubular space is large.

Mazzetti (27) confirmed Friedman's report for *Rana fusca*. He stated that in the fall, when all stages of spermatogenesis are found, there is an abundance of interstitial tissue. Toward the end of October spermatogenesis ceases and the interstitial cells diminish little by little until they are no longer demonstrable. He does not state, as does Friedman, that spermatozoa are not present at this time, but only reports that no spermatogenesis is taking place.

Chart II is based upon Friedman's report of *Rana fusca* together with information supplied by Mazzetti. It shows very well that the increase in size of the testis with spermatogenesis is accompanied by interstitial cell decrease. It also clearly indicates that the interstitial cell increase follows mating and does not precede it.

In *Rana viridis*, now known as *Rana esculenta*, Friedman observed all stages of spermatogenesis during late summer and fall. From June to October most of the tubules are small. After this spermatogenesis takes place. During early August the interstitial cells are well developed. In winter, when spermatogenesis continues and the tubules are distended, interstitial cells are no longer present. Mazzetti also made observations on the testes of this frog and reports that the interstitial cells are abundant during the period of intense spermatogenesis (time not given, nor are his criteria for intense spermatogenesis stated). His work is not thorough and is confined to the fall season.

Champy (7) observed that in *Rana esculenta* during July the interstitial cells undergo a regressive change and take on the aspect of connective tissue cells. Spermatogenesis is then most active. In autumn, when spermatogenesis is arrested,

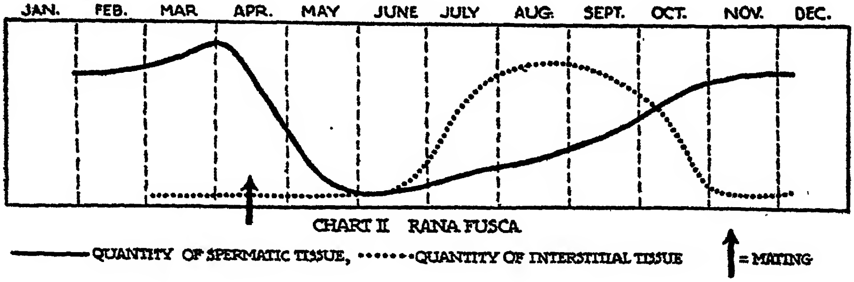


CHART II RANA FUSCA

the interstitial cells little by little become granular and increase both in number and in volume. This increase continues until January, when fat granules fill the cytoplasm of the interstitial cells. He traces the fat from these cells into the tubules during the following months. Mating takes place in April and May, and at this time the interstitial cells are at their minimum. After mating the interstitial cells rapidly increase. The tubules are empty in June. Spermatogenesis proceeds rapidly during the first part of July, and with equal abruptness the interstitial cells, deprived of their fat, return to fibroblasts. *Rana esculenta* resembles *Rana fusca*. The differences are matters of detail only.

interstitial cells increase after the mating season when the tubules have been emptied of sperm. Chart III from Champy's data on *Rana temporaria* shows that interstitial cell increase follows mating and accompanies ejection of spermatozoa from the lobules.

Friedman found that in the tree frog (*Hyla arborea*) the tubules are full of dividing cells throughout the month of July and the intertubular space is then very small. It contains only a few interstitial cells here and there among the connective tissue cells. In September, when spermatozoa are formed, the interstitial tissue is very rich and contains much fat. In October most of the tubules contain only spermatozoa, the quantity of intertubular

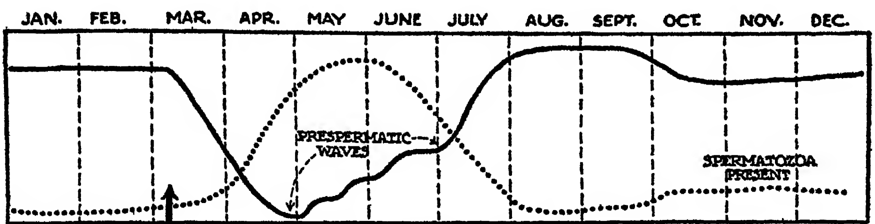


CHART III RANA TEMPORARIA

——— QUANTITY OF SPERMATIC TISSUE, ······ QUANTITY OF INTERSTITIAL TISSUE ↑ =MATING

In another paper (8) Champy presents all data collected by himself together with a very good review of the literature on Amphibia. His charts show the quantity of interstitial cells, but they do not give an exact picture of the quantity of spermatogenic tissue. In *Rana esculenta* for example, there is no spermatogenic tissue present immediately before or during mating. This is because Champy has presented intensity of spermatogenic activity and not quantity of germinal tissue. He states (8, p. 25) that in *Rana temporaria* the variation is still more marked than in *Rana esculenta* because only one wave of spermatogenesis takes place each year. Here again the fact is made clear that the

tissue is increased, and the interstitial cells are full of fat. According to Champy (8) *Hyla arborea* breeds in April, not in September or October. Friedman was apparently observing fall spermatogenesis, common to Anura, and in some way became confused regarding the mating season. Friedman also reported that in the toad (*Bufo vulgaris*) the interstitial tissue reaches its greatest development during spermatogenesis. These findings were confirmed by Mazzetti (27) in a general paper almost completely lacking in data. But Champy's (8) careful study shows that these authors apparently erred in their reports. He states (p. 262) that the testicular changes in *Bufo vulgaris*

resemble those of other Anura, and a chart built from his observations is herewith presented. See Chart IV.

Champy also reports that interstitial tissue is abundant during winter in *Rana esculenta*, *Hyla arborea*, *Bufo calamita*, *B. vulgaris*, *B. pantherina*, and *Alytes obstetricans*. Similarly he found that prespermatogenesis takes place throughout the year in each of these frogs and toads except *Alytes*.

Urodeles are much like anurans in

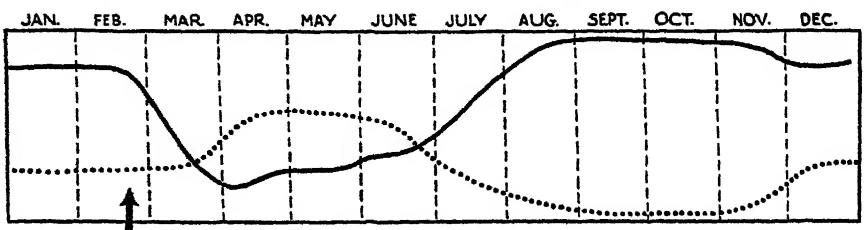


CHART IV BUFO VULGARIS

——— QUANTITY OF SPERMATIC TISSUE, ········QUANTITY OF INTERSTITIAL TISSUE ↑=MATING

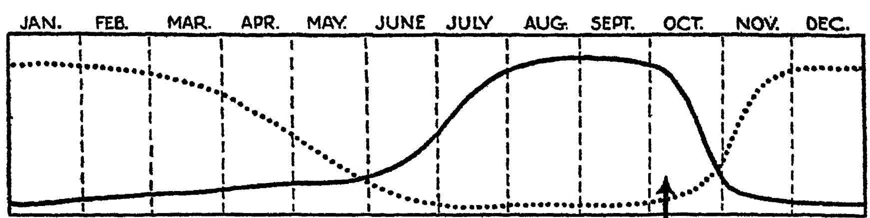


CHART V. NECTURUS MACULOSUS

——— QUANTITY OF SPERMATIC TISSUE, ········QUANTITY OF INTERSTITIAL TISSUE ↑=MATING

respect to testicular modifications. Champy emphasizes this similarity, and Chart V of *Necturus maculosus*, constructed from Humphrey's data, shows that this is true. Champy noted that in *Salamandra maculosa*, *S. atra*, and *Amblystoma tigrinum* interstitial cells appear after the spermatozoa are expelled. When spermatogenesis takes place they degenerate.

Champy places emphasis upon prespermatogenesis, found in both anurans and urodeles. He states that in anurans this endocrine function is performed by the interstitial gland, but he adds that it is difficult to admit that the interstitial tissue is endocrine in function (8, p. 266) because he was unable to find the supposed relation between the development of secondary sex characters and the development of the interstitial tissue (p. 270). He therefore believes that in those anurans having prespermatogenesis the hormone is produced by this abortive spermatogenesis. Champy looks upon prespermatogenesis, especially in urodeles, as a process of forming a "*corpus jaune testiculaire*," which produces the hormone. He states (8), however, that these bodies develop after the appearance of the secondary sex characters.

Humphrey (21, 22, and 23) has made a very complete study of the interstitial cells in urodeles. He reports that in *Necturus maculosus* few or no spermatozoa are present in the testis during the winter. These entirely disappear from the testis before the end of the following April. Spermatogonial division may be seen dur-

ing the winter. In the spring and early summer division and growth of germ cells take place. By October spermatozoa are mature, and at the end of that month the greater portion of the testis is again empty. The testis during July, August, and September is at the greatest size it attains at any time. The lobules are then enlarged and angular rather than circular, with blood vessels occupying the spaces where three or more tubules meet. No cells recognizable as interstitial cells can be found at this time. In late October the interstitial cells are developed from stromal cells, a process beginning in the caudal portion of the testis following departure of mature spermatozoa. According to Humphrey their development is to be looked upon as correlated with the regressive phase of spermatogenesis and not as a seasonal condition. The development of interstitial cells normally occurs following emptying of the lobule.

What has been given above for *Necturus* is true in general for *Cryptobranchus, Plethodon, Diemyctylus, Splerepes, Gyrinophilus,* and *Desmognathus*. Moreover, in some of these species interstitial cells completely disappear while, and even before, spermatogenesis proceeds.

Chart V, built from data offered in Humphrey's papers, shows clearly, as stated by that author, that interstitial cell development follows degeneration within the lobule and that it is not a seasonal condition. He offers much data clearly analyzed in support of his conclusions. This chart shows that the breeding season must be carefully noted, for in this species the interstitial cells are abundant during spring, when most species breed, but are at a minimum during October, its true breeding season. In a recent communication Humphrey states that he "is not sure that the breeding period has been clearly established. Animals have sperm in their vasa deferentia for some time after the testis empties. Necturus males are *capable of mating* in spring as well as in the fall. This is also true of *Plethodon, Diemyctylus, Spelerpes,* and other urodeles. The mating season may extend over several months."

Aron (3, p. 25) stated that of the divers elements of the testis only the glandular tissue parallels the seasonal evolution of sex characters. This glandular tissue develops by multiplication of Sertoli cells within a cyst (lobule of other authors). The connective tissue cells of the cyst wall also increase. The cyst gradually comes to appear like a corpus luteum. Its walls soon disappear, the cells rapidly atrophy, and a cicatricial tissue with globules of fat is substituted. The formation of this gland as observed by Aron differs somewhat from that reported by Champy, but they both refer to this body as having an endocrine function. Aron states (3, p. 116) that when the sex characters are present the gland is present and that when the gland is present the sex characters are present. This might well be a coincidental affair, but in Aron's hands experimental evidence appears to give it some significance. When he has cauterized this tissue without injury to the remainder of the testis the secondary sexual characters disappear. When the remainder of the testis is removed without injury to this organ the secondary sex characters pursue the normal course. However, the evidence is not conclusive because (1) it is almost impossible to cauterize this portion of the testis without injuring the blood supply to the remainder of the testis and (2) the change resulting from cauterization of this tissue is only a slight speeding up of the disappearance of characters that are soon to disappear as a normal process. Humphrey has also called my attention to the fact that in cauterizing this tissue the

operator is essentially destroying all the germinal tissue and that only empty lobules remain. It is further weakened by the fact that the appearance of secondary sex characters in urodeles just approaching sexual maturity must await the evacuation of the cysts following one spermatogenic cycle, for according to Aron (3, p. 112) only the evacuation of the cysts will introduce the genesis of this endocrine mass.

Humphrey shows that Aron's abortive spermatogenesis and Champy's prespermatogenesis vary in quantity. They are present only in certain species and not always in these. He draws attention to the fact that in testes of urodeles, as of other vertebrates, unfavorable environment causes injury to the germ cells and their degeneration follows. From data presented (Humphrey, 23) the conclusion that this germ cell degeneration is the result of unfavorable conditions in winter seems justified. This does not end in the formation of a true anatomical organ, and there is no need to ascribe a definite function to the degenerating lobules or associated interstitial cells. From this alone it cannot be said that the tissue does not perform a function. But if an endocrine function be ascribed to this tissue it can apply to only a limited number of species, and in these during part of the year. Its limited occurrence makes it seem very improbable that such tissue has an endocrine function in any species.

MODIFICATIONS IN TESTES OF BIRDS

In birds the testicular structure resembles very much that found in mammals. The germinal tissue is found in seminiferous tubules, where waves of spermatogenesis may be seen. The intertubular tissue is composed of lymph and blood vessels, nerves, connective tissue, and some interstitial cells.

Many early investigators reported volumetric and weight changes in birds during the year. Gadow (16) refers to the familiar fact that the testis of the house sparrow enlarges from the size of a seed during winter to that of a cherry during the mating season, at which time it displaces the digestive organs. Disselhorst (14) discusses the increase in volume of the testis approaching the time of mating. In *Fringilla* there is an increase in weight of about three hundred fold. He also cites Leuchhart as finding an increase in weight of one hundred and ninety fold in the Starling from winter to spring. In these reports, cytological data is lacking and only macroscopic information is given.

Stieve (32) reports that in the European Jackdaw (*Colaeus monedula collaris*) there is a fluctuation of four hundred and eighteen volumes in the testis during the year. This volumetric fluctuation is produced by changes in quantity of germinal tissue. In spring the testes increase in size up to April. At this time the tubules are greatly distended with germ cells, and it is then that mating takes place. Thereafter the testes decrease in volume until they reach a minimum size in January. The intertubular tissue is most abundant when the germ cells are at a minimum during winter. It is most abundant during the non-sexual period and least abundant at the time of mating. He refers to the increase in intertubular tissue as an interstitial cell hypertrophy. He is sure that the interstitital cells do not produce the testicular hormone because they are at their minimum when sex activity is at its maximum.

Parhon and Parhon (29) reported that in the goose (of the race Rouen) the testis diminishes in volume about the first of August. The spermatogenic tissue then becomes less abundant, and its cells

divide less actively. The tubule cells are at this time charged with fat granules. The intertubular tissue is more developed than in spring, and the interstitial cells, like the tubule cells, are charged with fat granules. This condition resembles that reported by Champy for Amphibia.

Benoit (5 and 6) states that during the winter while the testis (of *Cambasson*) is in repose it contains spermatogonia and Sertoli cells. At the beginning of the sexual period in spring the seminiferous tubules enlarge a little. They slowly gain in volume as spermatogenesis increases. During the early period of development spermatocytes make their appearance, and then later spermatids are found. Only when *Cambasson* is fully active sexually are spermatozoa present, and at this time the testis is maximum in size.

He states that interstitial cells are very abundant during winter, when spermatogenesis has ceased. They then contain fat granules. Toward spring many connective tissue cells become enlarged. Some contain fuchsinophile spherules. When sex activity is at its height these interstitial cells are relatively much less abundant than during winter and early spring. They change in cytological structure, becoming, he thinks, glandular. He finds no volumetric parallelism between the interstitial cells and sex activity and endeavors to find a parallelism in the cytological changes seen at this time. These cytological modifications were briefly pointed out by Parhon and Parhon, but these authors were not led to believe that these cells were more secretory during the period of sex activity than during the inactive period. Many investigators are inclined to look upon these changes as showing that the interstitial cells are trophic bodies for the tubule cells. See Saintmont (33) and Tandler and Grosz (34). Others view them as consequences of changes in size of the tubules rather than from a teleological aspect. See Whitehead (40), Kuntz (24), Humphrey (21), and Oslund (28).

It is quite evident that sex activity in birds is pronounced during the period of spermatogenesis. At that time the testes are enlarged as compared with the inactive period. On the other hand there is an increase in the number and volume of interstitial cells during the period of sexual *in*activity. Plumage is usually more brilliant during the time that spermatogenesis is most active and is dull following the autumnal molt, when the interstitial cells are abundant. The parallelism between spermatogenesis and sexual activity is evident, while there is an inverse relationship between sexual activity and interstitial cells.

MODIFICATIONS IN TESTES OF MAMMALS

In testes of mammals the germinal epithelium is found in seminiferous tubules. Spermatogenesis proceeds in waves, and all of its stages may be found in each tubule. Between the tubules are found nerve elements, blood and lymph vessels, and connective tissue cells. Some of the connective tissue cells are typical fibroblasts, while others are large and contain an abundance of cytoplasm with fuchsinophile granules. It should be emphasized that not all connective tissue cells are interstitial cells, nor is the intertubular space always filled with interstitial cells nor even with fibroblasts. It often contains much lymph and always has blood and lymph vessels and nerve elements. Of all the intertubular tissue only the interstitial cells are supposed to elaborate a glandular product.

Hansemann (19) reported that in the Marmot (*Marmota marmota*) there is no trace of spermatogenesis during hiberna-

tion. There are at this time some interstitial cells, but they are not abundant. He found them abundant during the summer. Ganfini (17) repeated and extended the work on marmots. He found the interstitial cells as abundant in winter as in the sexually active season. He stated that they were more nearly round in winter and appeared to be secreting less actively.

Rasmussen (30) made a complete study of hibernation effects upon the testis in *Marmota monax*. From his data it seems that spermatogenesis progresses slowly during the late fall and winter months. In early March the spermatogenic activity increases markedly and reaches its height during the latter part of March and the first part of April. Thereafter spermatogenesis quickly subsides, and in June and July it is at its lowest point. From September on it again progresses slowly.

Interstitial cell hypertrophy starts just before mating, and the cells reach their maximum development after spermatogenesis has ceased and the tubules are empty. They remain well developed until July, at least two months after the cessation of the spermatogenic cycle. The mating season is during late March and early April, and young are born during the first part of May. Mating thus follows the great wave of spermatogenesis and precedes the crest of interstitial cell hypertrophy. See chart VI.

Regaud (31), Lecaillon (25), and Tandler and Grosz (34) have made a comprehensive study of the seasonal changes in the testis of the mole (*Talpa europea*). From their work it is evident that spermatogenesis proceeds in autumn and winter. The spermatogenic activity increases during late February and attains its height during March. At this time the testis is three times its usual diameter, and this increase results entirely from increase in germ cells. Rutting is during March, and by the end of the month most of the sperm are gone and the testis again decreases in size. Thereafter it reaches a low ebb in July, when only a syncytium of Sertoli cells and a few spermatogonia remain in the tubules. The interstitial cells are minimal during February and March. They increase immediately after mating, when the sperm are gone. When spermatogenesis again takes place in the fall the interstitial cells decrease, though they are still numerous during the winter according to Lecaillon.

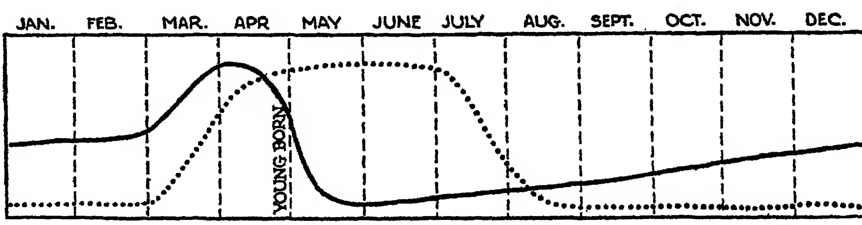


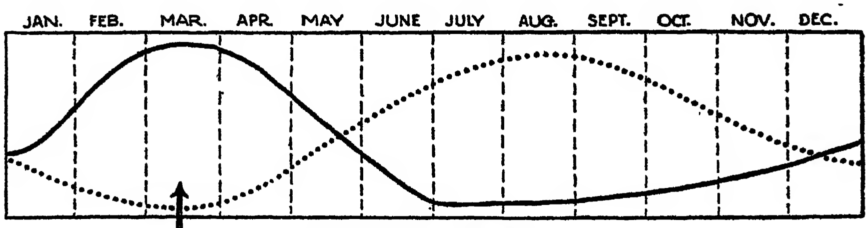
CHART VI MARMOTA MONAX

——— QUANTITY OF SPERMATIC TISSUE, ········ QUANTITY OF INTERSTITIAL TISSUE

In moles it is quite evident that interstitial cell hypertrophy occurs when spermatogenesis is minimal and the tubules empty. It does not precede mating but follows it. This is clearly shown in chart VII herewith presented.

According to Marshall (26) testes of the Hedgehog (*Erinaceus europeus*) begin to increase in size about the end of March, and by the middle of April they are

considerably enlarged. Active spermatogenesis is found in April, and free spermatozoa are present in the genital passages at the end of the month. Spermatogenesis continues until September, and from then on the testes decrease in size. According to this investigator the quantity of interstitial cells runs parallel with spermatogenesis. The increase in size of the testis, he says (26, p. 253) is due partly to the increase in the size and number of seminiferous tubules, but even more matogenesis. Part of the intertubular increase is due to the increase in the vascular bed, as Marshall has observed, but part appears to be due to interstitial cell increase. A study of the Hedgehog alone might lead one to infer that the interstitial hypertrophy paralleling spermatogenesis and sex activity had something to do with the increased sex activity of that period. Such an inference is not justified because this parallelism is not found in other species. Tandler and



TALPA EUROPEA – CHART VII

——— QUANTITY OF SPERMATIC TISSUE, ······· QUANTITY OF INTERSTITIAL TISSUE ↑ = MATING

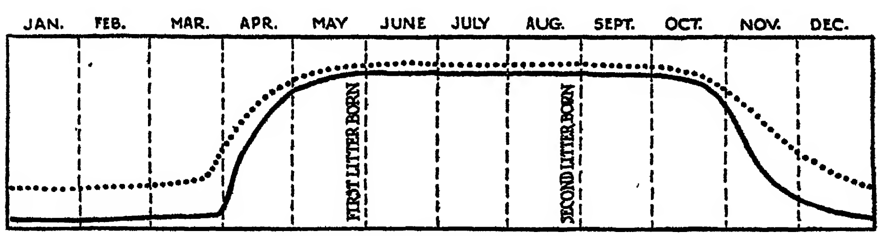


CHART VIII ERINACEUS EUROPEUS

——— QUANTITY OF SPERMATIC TISSUE, ······ QUANTITY OF INTERSTITIAL TISSUE

to proliferation of interstitial cells. This results in wide separation of the tubules. Blood vessels of considerable size are not uncommon, but they disappear when retrogression sets in. Rasmussen states that there is an actual increase in the number of interstitial cells during part of the spermatogenic wave in marmots, which his chart shows reaches its maximum after mating. Spermatogenesis continues during the summer in the Hedgehog, and in this species the interstitial cell hypertrophy therefore parallels spermatogenesis.

Grosz found that in the mole the only parallelism present is between spermatogenesis and sex activity. This parallelism is constant in all mammals. The quantity of interstitial cells in moles is at a minimum during sex activity, and in marmots they reach a maximum only after birth of young. This is long after mating has ceased. To function as activators of sex activity the interstitial cells should develop prior to or at the same time as spermatogenesis. As a matter of fact their increase follows sex activity.

DISCUSSION

When the data on fishes are carefully assembled no correlation is found between the volume of the interstitial cells and time of sex activity. Such a parallelism was reported by Courrier, but Champy and Van Oordt have both shown this to be an error. In Amphibia such a parallelism was reported by Friedman and by Mazzetti for *Rana fusca*, *Rana viridis*, and *Hyla arborea*. When the data have been carefully analyzed it becomes apparent that the interstitial cells reach their maximum volume some time after mating. Champy failed to find a parallelism between interstitial cell volume and sex activity and sought other possible parallelisms. Humphrey has shown that in urodeles the interstitial cell increase is related to emptying of lobules and not to sex activity. Aron stresses the presence of Sertoli cells in the "Glandular masses" which alone form the hormone in urodeles. In birds it is certain that the interstitial cells do not increase in volume before or during the period of sex activity. They are most abundant when sex activity is least evident. In mammals the evidence is indicative of the same relationship. It was pointed out above that Marshall found an interstitial cell increase during spermatogenic activity in the Hedgehog. The interstitial cells increase before sex activity and decrease during hibernation. Rasmussen reported that in *Marmota monax* there is an increase of interstitial cells that begins before mating. But the interstitial cells are most abundant at the time of or after birth of the young. The maximum volume therefore lags behind actual mating rather than precedes it. Ganfini found that in *Marmota marmota* the interstitial cells were as abundant during winter as during the sexually active period. There is then no real parallelism between sex activity and interstitial cell volume in *Marmota*. In the mole it is certain that the interstitial cells are least abundant during the mating season. They increase when spermatogenesis is arrested, and this is after mating.

It is therefore clear that there is no constant parallelism between sex activity and interstitial cell quantity. In fact there is in most cases an inverse relationship. The only exceptions to this state of affairs are in *Erinaceus europeus* and possibly in *Marmota monax*. In the former an exact relationship between sex activity and interstitial cell quantity is reported, while in the latter the interstitial cell increase begins during the period of sex activity and reaches its maximum after young are born. It appears more reasonable to claim that the parallelism found in these two species is an accidental relationship while that found in all other species cited above is typical rather than to use these two species as typical of vertebrates.

The inverse relationship between sexual activity and quantity of interstitial cells takes on added importance when it is noted that there is a decrease in or abeyance of sexual activity at the time that the interstitial cells increase. In some species they are present only during the season of sex inactivity. Nor should their entire absence in certain species be overlooked. These facts stand in direct opposition to the interstitial cell secretory theory.

In the group of animals in which the interstitial cells are present only during the period of sex inactivity it might be argued that the hormone is effective only after a certain latent period. There are no data available that show how long it takes the hormone to become effective, but it is known that its absence is evident in 5 to 12 days in rats (Hoskins, 20) and in about the same period in birds when determined

by changes in feathering. The period between the disappearance of interstitial cells and the onset of sexual activity is so long that it seems improbable that the interstitial cells had any relation to sex desire and mating behavior.

It must be admitted that the methods of determining quantitative amounts of interstitial cells have not been accurate. This has been pointed out by Bascom (4). The authors have offered them as relative quantities and in such a sense they have shown the gross changes met with. One error is present throughout the early work that might explain some of the minor discrepancies seen in the various reports; namely the failure to distinguish between intertubular and interstitial tissue. Nor is this error corrected by the use of Bascom's method. It is difficult to make sure of estimating an increase in interstitial cell quantity and number in any way short of actually measuring and counting the individual cells. But careful quantitative estimations of interstitial cell increases do not appear necessary. According to Lipschutz (41) one-sixteenth of a testis produces enough hormone to keep the animal normal. It is also known that the testicular grafts will promote the normal development of male rats, guinea pigs, or birds. Small variations are therefore not important.

Are there cytoplasmic or nuclear changes paralleling the periods of sex activity that might indicate which cells secrete the testicular hormone? The change from fibroblast to interstitial cell is marked by the appearance of fuchsinophile granules in the cytoplasm and the inclusion of much fat. But this occurs during the post-active period according to the data reviewed above. Benoit found that the interstitial cells of *Cambasson* decrease in quantity during the season of sex activity, but he believes that they become more glandular at this time. They contain voluminous spherules which produce a fuchsinophile secretion. The supporters of the interstitial cell secretory theory, after noting what they thought was a parallelism between sex activity and interstitial cell increase, postulated that these cytoplasmic inclusions were the hormone products being formed in the cells. No proof has been offered in support of this supposition. Now Benoit and others turn about and postulate that since certain cells contain fuchsinophile granules they must be secretory cells. They must first prove that such granules are hormonal products within the cell before they can argue that cells containing such granules are secretory cells. Parhon and Parhon noted that the interstitial cells in the goose become charged with fat granules, which they believed to be secretory material, but this occurs in the fall after mating has ceased. Champy found changes in the interstitial cells and in the Sertoli cells that indicated transfer of fat inclusions from the former to the latter. He concluded that the phosphorus fat elaborated by the interstitial cells serves as nutrition for the spermatozoa being formed in this tissue. He then postulates that in some mysterious manner the interstitial cells determine the development of the germ cell, presumably through the transfer of this secretory (fatty) material. Humphrey has very clearly shown that interstitial cell increase is related to emptying of spermatic tubules and that it is not a seasonal condition. Humphrey suggests that they may serve as a nutritional balance in the testis and also prevent a sudden collapse of the lobules and of the testis when sperm are ejected. Oslund (28) suggests that they are more strictly a result and ascribes to them no functional purpose.

The writer interprets Champy as stating

that in some anurans the interstitial cells produce the testicular hormone. But where prespermatogenesis is found the hormone is produced by this abortive spermatogenesis. In urodeles he believes that the hormone is produced by a "corpus jaune testiculaire," which is a product of the abortive spermatogenic process. Aron maintains that a "glandular body," which he describes as a product of Sertoli cell division, produces the testicular hormone in urodeles. Both of these authors therefore point to germinal elements as the chief source of the hormone production. Their individual theories are very much weakened by Humphrey's observations, which indicate that this abortive spermatogenesis in American urodeles is a result of unfavorable environment, that it is not present in many species and in those species where it is sometimes seen it is not constant. We cannot call this a parallelism but a coincidence, for which Humphrey has offered a satisfactory explanation.

There is, however, one parallelism that is constant in all species. A glance at the charts will make it apparent that there is always an abundance of germ cells, either developing or mature, immediately before and during mating. In all animals there is some germinal tissue throughout the year. It increases slowly after mating and becomes abundant when the next mating season approaches. In some species the increase immediately before mating is rapid, while in others it is more gradual. These are individual variations of cell activity, but in all vetebrates the germinal tissue is maximum in quantity at the time of mating. This of itself does not show that this tissue produces the testicular hormone. Spermatogenesis is the preparation of cells whose function is that of fertilizing the egg. But may not these anatomic and physiologic changes of mating be induced by a substance produced by the metabolic processes of these cells? This substance may be a waste product of cell metabolism or a by-product (an unused material) split off from the material furnished to the cell by the blood. We know, for example, that the lymph from the arm or leg differs from that of other parts of the body. This appears to be a result of the cell metabolism of the particular tissue concerned.

Germ-cell development is the only parallelism at present found between any particular testicular element and the physiological changes accompanying mating. Champy (10) states that though there is no positive demonstration there is presumptive evidence favoring a correlation between appearance of sex characters and maturity of spermatozoa in *Cysprinodentes varions*. The writer is not ready to commit himself to such a definite correlation. It seems that the presence of any *active germinal epithelium* is sufficient to insure what is commonly thought of as hormonal activity.

The charts for this paper were made in the Illustration Studios of the University of Illinois College of Medicine and Dentistry.

LIST OF LITERATURE

(1) Aron, M. 1921. Sur l'existence et le rôle d'un tissu endocrinien dans le testicule des Urodeles. Heb. de Sci. de l'Acad. de Sciences, 173: 57–59.

(2) ———. 1921. Sur le conditionnement des caractères sexuels secondaires chez les Batraciens Urodeles. Compt. rend. Soc. de Biol., 85: 482–484.

(3) ———. 1924. Recherches morphologiques et expérimentales sur le déterminisme des caractères sexuels mâles chez les Urodeles. Arch. de Biol., 34: 1–163.

(4) Bascom, K. F. 1925. Quantitative studies of the testis. Anat. Rec., 30: 225–241.
(5) Benoit, J. 1923. Sur les modifications cytologiques des cellules interstitielles du testicule chez les oiseaux à activité sexuelle périodique. Compt. rend. Soc. de Biol., 88: 202–205.
(6) ———. 1923. Sur les variations quantitatives des tissus interstitiels glandulaire et non glandulaire dans le testicule des oiseaux à activité sexuelle périodique. Compt. rend. Soc. de Biol., 88: 205–207.
(7) Champy, C. 1908. Note sur les cellules interstitielles du testicule chez les batraciens anoures. Compt. rend. Soc. de Biol., 64: 895–896.
(8) ———. 1913. Recherches sur la spermatogenèse des batraciens et les éléments accessoires du testicule. Arch. de Zool. Exper., 52: 13–304.
(9) ———. 1913. De l'existence d'un tissu glandulaire endocrine temporaire dans le testicule. Compt. rend. Soc. de Biol., 74: 367–368.
(10) ———. 1923. Observations sur les caractères sexuels chez les poissons. Compt. rend. Soc. de Biol., 88: 414–417.
(11) ———. 1924. Sur les conditions qui reglent la quantité des variants sexuels. Compt. rend. Soc. de Biol., 90: 37–39.
(12) Courrier, R. 1921. Étude du déterminisme des caractères sexuels secondaires chez les poissons. Arch. d'anat., d'histol. et d'embryol., Strassb., 1: 119–144.
(13) ———. 1921. Sur le conditionnement des caractères sexuels secondaires chez les poissons. Compt. rend. Soc. de Biol., 85: 486–488.
(14) Disselhorst, R. 1908. Gewichts-und Volumzunahme der männlichen Keimdrüsen bei Vögeln und Säugern in der Paarungszeit. Anat. Anz., 32: 113–117.
(15) Friedman, F. 1898. Beiträge zur Kenntniss der Anatomie und Physiologie der männlichen Geschlechtsorgane. Arch. f. mikr. Anat. 52: 856–891.
(16) Gadow, H. 1896. Newton's Dictionary of Birds—Reproduction.
(17) Ganfini, C. 1903. Les cellules interstitielles du testicule chez les animaux hibernants. Arch. Ital. de Biol., 40: 323.
(18) Geiser, S. W. 1922. Seasonal changes in the testis of *Gambusia affinis*, the top-minnow. Anat. Rec., 23: 104–105.
(19) Hansemann, D. 1895. Über die sogenannten Zwischenzellen des Hodens und deren Bedeutung bei pathologischen Veränderungen. Arch. für Path. Anat., 142: 538–546.
(20) Hoskins, R. G. 1925. The effect of castration on voluntary activity. Am. Jour. Physiol., 72: 324–330.
(21) Humphrey, R. R. 1921. Interstitial cells of the urodele testis. Am. Jour. Anat., 29: 213–279.
(22) ———. 1922. Multiple testis in urodeles. Biol. Bull., 43: 45–67.
(23) ———. 1925. A modification of the urodele testis resulting from germ cell degeneration. Biol. Bull., 48: 145–165.
(24) Kuntz, A. 1919. Experimental degeneration in the testis of the dog. Anat. Rec., 17: 221–234.
(25) Lecaillon, A. 1909. Sur les cellules interstitielles du testicule de la taupe. Compt. rend. Soc. de Biol., 66: 599–601.
(26) Marshall, F. H. A. 1911. The male generative cycle in the hedgehog; with experiments on the functional correlation between the essential and accessory sexual organs. Jour. Physiol., 43: 247–260.
(27) Mazzetti, I. 1911. I caratteri sessuali secondari e le cellule interstigiale del testicolo. Anat. Anz., 38: 361.
(28) Oslund, R. M. 1925. Interstitial cell hypertrophy. Am. Jour. Physiol., 69: 589–598.
(29) Parhon, C. I., and Parhon, C. 1922. Sur l'involution estivale des caractères sexuels secondaires du plumage chez le canard mâle et sur les modifications parallèles du testicule chez le même animal. Compt. rend. Soc. de Biol., 87: 1227–1229.
(30) Rasmussen, A. T. 1917. Seasonal changes in interstitial cells. Am. Jour. Anat., 22: 475–515.
(31) Regaud, C. 1904. État des cellules interstitielles du testicule chez la taupe pendant la période de spermatogenèse et pendant l'état de repos des canalicules séminaux. Compt. rend. de l'Assoc. d'Anat., 56: 54.
(32) Stieve, H. 1921. Neue Untersuchungen über die Zwischenzellen. Anat. Anz., Ergnssheft., 54: 63–76.
(33) Saintmont, G. 1905. Recherches relative à l'organogenèse du testicule et de l'ovaire chez le chat. Arch. de Biol., 22: 71–161.
(34) Tandler, J., and Grosz, S. 1911. Über den Saisondimorphismus des Maulwurfhodens. Arch. f. Entw. der Organ., 33: 297–302.
(35) ———. 1912. Über den Saisondimorphismus des Maulwurfhodens. Arch. f. Entw. der Organ., 35: 132.

(36) Turner, C. L. 1919. The seasonal cycle in the spermary of the perch. Jour. Morph., 32: 681–711.

(37) Van Oordt, G. J. 1924. The significance of the interstitium testis in fishes. Proc. Kon. Akad. Wetensch. Amsterdam, 27: 161.

(38) ———. 1924. Die Veränderungen des Hodens während des Auftretens der sekundären Geschlechtsmerkmal bei Fischen. Arch. Mikr. Anat. Entwick., 102: 379–405.

(39) Van Oordt, G. J. 1925. The relation between the development of the secondary sex characters and the structure of the testis in the teleost. Brit. Jour. Exper. Biol., 3: 43–59.

(40) Whitehead, R. H. 1904. The embryonic development of the interstitial cells of Leydig. Am. Jour. Anat., 3: 167–182.

(41) Lipschutz, A., and Ottow, B. 1920. Sur les conséquences de la castration partielle. Compt. rend. Soc. de Biol., 83: 1340–1341.

EVOLUTION AND MORTALITY

By

RAYMOND PEARL

Institute for Biological Research, Johns Hopkins University

THE PROBLEM

IN 1920, in an attempt to approach the problem of human mortality from a more rational standpoint than that of current vital statistics, I (8) discussed the distribution of human deaths on the basis of an organological classification of the several statistically recorded causes. The underlying idea in the classification was to group all causes of death under the heads of the several organ systems of the body, the functional breakdown of which is the immediate or predominant cause of the cessation of life. The basis of the classification was not that of etiology, but rather that of the anatomical location of the principal breakdown. The matter was further discussed and the original classification amended and corrected in later publications (9, 10).

In these investigations there came to light evidence that the present characteristics and distribution of human mortality are in part—perhaps a considerable part—the results or consequences of the evolutionary history of the human body itself. It appeared that the different organ systems of the body are not all equally capable of withstanding the environmental stresses and strains which they have to meet. The evidence on this point was necessarily suggestive rather than conclusive. Human vital statistics, taken by themselves, are for many reasons inadequate to elucidate such a point as this. It demands a study of the evolutionary progression which has occurred in respect of mortality among the animals lower in the scale than man, who represents only the final end term in the series. The real question, on which we should like to have evidence is: How do the relative mortalities chargeable to breakdown of each of the different organ systems of the body compare among the different orders of animals, including man?

What obviously is needed to answer the question is a record of the comparative pathological anatomy of the different orders of vertebrate animals. Unfortunately there does not exist anything like a complete or detailed body of knowledge regarding the pathology of wild vertebrate animals living in a natural state. There are several reasons for this lack, besides the obvious one that few persons have particularly interested themselves in such study. The wild animals that happen to be killed by hunters are the survivors of a steady process of natural selection, and are therefore apt to be in an excellent state of health. The sick, weak and defective have long since died off, under circumstances practically always making impossible post-mortem examination. Again wild animals probably only rarely die a natural death due to internal pathological changes. When an animal in a state of nature falls appreciably below par in health, sooner or later something kills it.

But while ideal material for comparative pathology is thus lacking, there is available a body of records which can be utilized to throw some light on our problem. I refer to the autopsy records made in large zoological gardens. The important conditioning factors regarding such records from a biometric point of view are these:

a. The population of a zoological garden is composed of wild animals. But in this population the different natural orders are not necessarily or actually represented in proportion to the frequency with which individuals belonging to these orders occur in a state of nature. The population is a selected one, the basis of the selection being primarily the behavior and longevity of the individuals in captivity, and their interest to human beings as objects of display. This artificial character of a zoological garden population means that deductions regarding mammals as a group, or birds as a group, must always be subject to the reservation that the samples are not completely representative.

b. The animals are in a state of captivity, artificially and regularly fed, in accordance with what human beings, on an insufficient basis of knowledge, suppose to be their needs and desires. That these conditions alter the whole natural and normal biological picture, including its pathological aspects, admits of no doubt. To paraphrase Dr. Johnson's remark about the performing dog the wonder is not that the animals live as well as they do in zoological gardens, but that they live at all under such unnatural circumstances.

c. In most zoological gardens complete and careful post-mortem examinations are not made of all the animals that die, and the results of such examinations as are made are not published in detail. An outstanding exception to the latter statement is furnished by the thorough and painstaking work of Fox (2) and his assistants at the Philadelphia Zoological Garden. Here a trained pathologist has taken the work seriously and amassed a collection of records of great interest and value. It is unfortunate that the statistical presentation of the records in the monumental report cited falls, in some respects, below the high level of excellence of the pathological work itself.

While these factors distinctly limit the usefulness, for the present purpose, of these records of deaths in zoological gardens, it is desirable to examine some of them briefly. In a comprehensive study of the biology of life duration and death any and all evidence, however fragmentary, should be brought under review.

DATA FROM THE LONDON ZOOLOGICAL GARDEN

From a biometric point of view the statistics of deaths in the Garden of the Zoological Society of London, are the most satisfactory. Their outstanding merit is that they account, in some way or other, for *all* the deaths occurring within a given year. The record is statistically complete. It is in this respect that the death records from the National Zoological Park in Washington, published in the Annual Reports of the Smithsonian Institution, fail. In a quite erratic way they leave a considerable number of deaths unaccounted for.

The present paper is based upon the statistics from the London Gardens for the four years 1920 to 1923 inclusive, as published by N. S. Lucas, M.B., F.Z.S. (4–7), the pathologist to the Society during the years named.

In these four years 4,448 deaths in total were reported. Of these 3,150 were recorded by causes, as determined by

autopsy, for mammals, birds, and reptiles. The remainder fell into Class X (*cf. infra*), incapable of organological classification. Individuals not autopsied are accounted for under such rubrics as "Eaten by rats;" "Decomposed;" "Not examined." Besides these there is the rubric "Killed," which includes those animals killed by other animals. Those killed on order, because of illness or for other reasons, are distributed to causes according to the results of the autopsy examination. Other rubrics are "Not diagnosed;" "Exposure." The number of deaths under these and other organologically unclassifiable rubrics, such as "Debility," is large in the case of reptiles, less in birds, and much smaller in the mammals. In dealing with the material one is obliged to assume that these deaths constitute in part a random sample, in respect of pathological causation, of all deaths; or, in the case of purely accidental deaths, are of entirely healthy individuals. In the second of these alternatives the deaths obviously have no place in a *biological* classification. They simply do not come into the reckoning here, any more than with human mortality. As to whether the other organologically unclassifiable deaths are a random sample, pathologically speaking, of the total it is impossible to determine definitely. It seems probable that they are fairly so, for the reason that if one compares the statistics of different zoological gardens, in which the proportions of unautopsied or unrecorded deaths vary widely, it is found that the ratios between the different ascertained causes among the autopsied and recorded portion of the dead population are fairly constant from garden to garden. This could only happen, assuming honest and fairly careful autopsy work, as we are entitled to, if the unrecorded deaths approximated a random sample of all deaths in respect of their pathological characteristics.

The organological classification of the causes of death set up in (8–10) and followed in this present study is as follows:

I. Circulatory system, blood, and blood-forming organs.
II. Respiratory system.
III. Primary and secondary sex organs.
IV. Kidneys and related excretory organs.
V. Skeletal and muscular systems.
VI. Alimentary tract and associated organs concerned in metabolism.
VII. Nervous system and sense organs.
VIII. Skin.
IX. Endocrinal system.
X. All other causes of death.

TABLE 1

Deaths in London Zoological Garden, 1920–1923 inclusive

YEAR	MAMMALS		BIRDS		REPTILES	
	I-IX	X	I-IX	X	I-IX	X
1920	273	63	369	103	148	113
1921	169	38	392	121	163	109
1922	261	58	434	147	119	107
1923	241	90	443	196	138	153
Totals	944	249	1,638	567	568	482

The actual numbers of the 4,448 deaths in the London Zoological Garden, here dealt with, falling respectively into Classes I–IX inclusive, and Class X, are shown in table 1.

ORGANOLOGICAL DISTRIBUTION OF DEATHS

In table 2 the biologically classifiable deaths in the four years experience (1920–1923) of the London Zoological Garden are tabulated according to organ systems, on a percentage basis, the figures representing the number of deaths in each class per hundred deaths from all causes (exclusive of those falling in our Class X). For comparison the last two columns give corresponding figures for human beings. The first of these columns is from the mortality of the City of São Paulo, Brazil, in 1917, and the second from that of

England and Wales in 1914. England stands at the forefront of civilization in general and of health, hygiene and sanitation in particular. Man in England represents certainly a high product of human evolution. The population of São Paulo is, statistically speaking, a more primitive one, from both a general evolutionary viewpoint and from that of public health and sanitation, than that of England and Wales. To take but a single example by way of evidence in support of this statement, the official records state that 18.2 per cent of the persons married in the City of São Paulo during the year 1918 were illiterate (unable to read or write).

In one respect the figures in the last two columns of table 2 differ from those previously published (8, 9 and 10) for the same population. In the original treatment of the human material on the basis of organological classification of the mortality a portion of the deaths of infants recorded as due to "premature birth" and to "injuries at birth" were included with the deaths falling in Class III, Primary and Secondary Sex Organs. The reasons for so assigning those deaths were fully discussed in the publications cited. But plainly there is nothing in the mortality of lower animals, as recorded in zoological gardens, which corresponds to the infant mortality. So then the deaths due to these causes were subtracted out of the totals of Class III in making up the last two columns of table 2. The residue is more nearly comparable with the mortality placed in this class in the case of the lower animals.

The first thing which strikes one, upon examining this table, is that broadly the distribution of mortality to organ systems runs parallel in the three orders of lower animals to the condition found in man. This is shown graphically in figure 1.

TABLE 2

The distribution among the different organ systems of each 100 biologically classified deaths

GROUP NUMBER	ORGAN SYSTEM	REPTILES	BIRDS	MAMMALS	MAN (SÃO PAULO 1917)	MAN (ENGLAND AND WALES 1914)
I	Circulatory system, blood	4.75	3.85	6.99	18.78	25.57
II	Respiratory system	32.99	37.33	46.19	26.94	33.44
III	Primary and secondary sex organs	2.11	2.87	0.64	2.22	3.86
IV	Kidneys and related excretory organs	0.88	4.52	3.92	5.29	4.03
V	Skeletal and muscular system	0	0.37	2.01	0.44	1.54
VI	Alimentary tract and associated organs	58.56	50.83	38.66	39.22	21.40
VII	Nervous system and sense organs	0	0.12	0.64	6.52	8.91
VIII	Skin	0.70	0	0.32	0.51	1.01
IX	Endocrine system	0	0.12	0.64	0.07	0.23
	All biologically classified deaths	99.99	100.01	100.01	99.99	99.99

It is seen at once that in reptiles, birds, and mammals, just as in man, the two organ systems having the largest mortality chargeable to them are the respiratory and the alimentary systems, with the circulatory system standing third. The other organ systems, which have a low mortality chargeable to them in man, also are concerned in a low mortality in the reptiles, birds, and mammals. This rough, but still evident correspondence between man and the lower orders of vertebrates in the organological distribution

of their mortality considerably tends to increase one's confidence that this classification of mortality has some real biological significance.

This confidence is further increased if table 2 is studied in detail. Let us consider first Class II, the mortality attributable to breakdown of the respiratory tiles. When we come to man this progression is broken. Respiratory mortality is here lower. The thought at once suggests itself that here is to be observed a result of man's intelligent control of his environment through housing, sanitation, and hygiene. It is at least conceivable that man's real biological position here

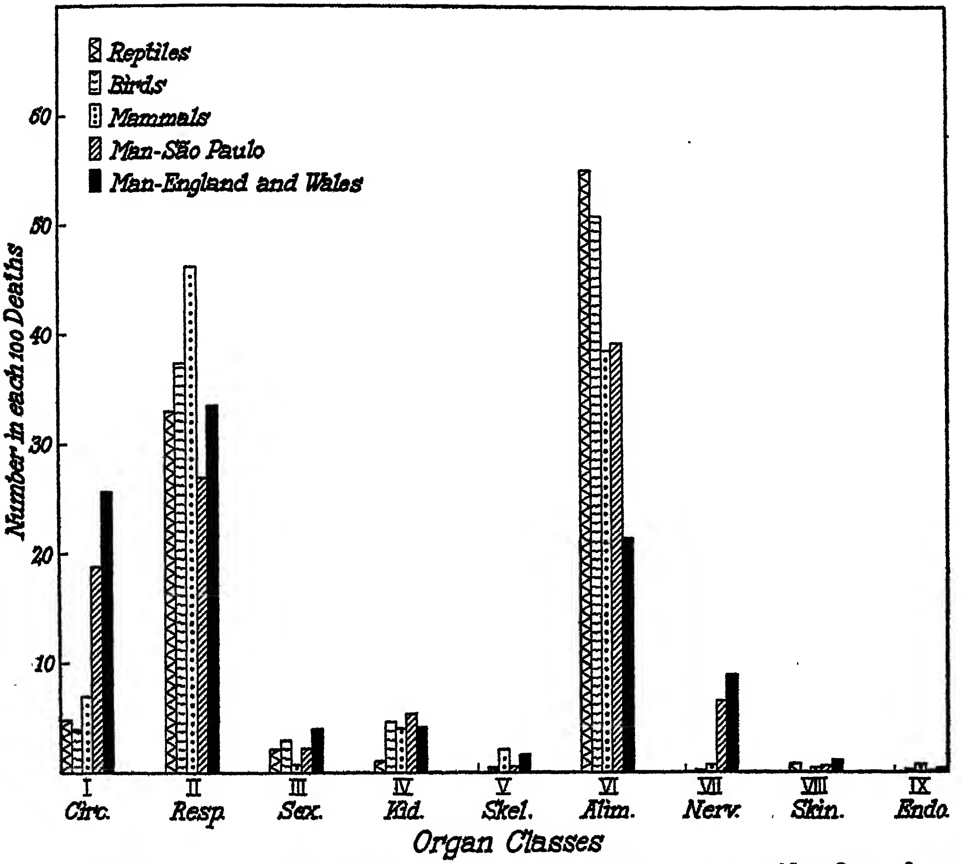


FIG. 1. THE MORTALITY, PER HUNDRED DEATHS FROM ALL CAUSES, DISTRIBUTED AMONG NINE ORGAN SYSTEMS, IN REPTILES, BIRDS, MAMMALS, AND MAN

system. It is seen that this mortality steadily and regularly increases proportionately as we pass from reptiles, through birds, to mammals. There appears to be a clear evolutionary progression here. The respiratory system of mammals appears to be less effectively adapted for coping with the environmental stresses and strains put upon it than it is in reptiles.

should be with a respiratory mortality as high or higher than that of the lower mammals. But because he has learned in some degree how to protect himself from respiratory infections, and to treat them so that they do not so often lead on to death, his actual observed respiratory mortality falls somewhat below that of the lower vertebrate orders.

If the mortality chargeable to the alimentary tract and its associated organs is examined in detail there is again seen to be a regular progression associated with advancing phylogenetic position. The proportionate mortality from diseases finding their seat in the alimentary tract and its associated organs is highest in the reptiles, lower in the birds, lower still in the mammals, and finally lowest in man living under superior conditions of present-day civilization (England and Wales). A human society less highly developed from the viewpoint of public health and hygiene (São Paulo) has a relative alimentary tract mortality identical with that of the mammals other than man.

There is another point which needs consideration in connection with the mortality charged against the alimentary tract. The figures of the last two columns of table 2, relating to man, are based upon deaths at all ages, including infant mortality. But in human infants, as I showed in table 11 of The Biology of Death (9, p. 136), it is the alimentary tract which is concerned in the largest proportion of fatalities, the percentage being 68.8 in the case of males and 40.6 in the case of females. In the figures of table 2 above relating to the lower forms, reptiles, birds, and mammals, there are included presumably very few if any deaths of extremely young animals. It is a not unreasonable inference that if "infant mortality" were included in the figures for animals the proportionate mortality chargeable to the alimentary tract would be even higher in reptiles, birds, and mammals than the figures actually available indicate.

There is a regular progression of increasing mortality chargeable to the nervous system as we go up the evolutionary scale, and the same thing appears to be true for the excretory organs, with some minor fluctuations in the figures not greater than might reasonably be expected by chance, where the numbers involved are so small. The tendency to increasing mortality from breakdown of the nervous system was long ago noted by Laycock (3) in his lectures on constitution in relation to disease. He said (p. 206): "Man as compared with other animals is peculiarly predisposed to degeneration of the nervous system; and civilized man, as compared with uncivilized."

Up to this point in the discussion the assumption has been that the deaths which failed of autopsy could be regarded as a fair random sample of all deaths, in respect of their pathology. But table 1 shows that the proportion of such unautopsied deaths to all deaths is much higher in the Zoological Garden experience than is the proportion of human deaths falling in our Class X to all human deaths. While the assumption made as to the random distribution pathologically of these undistributable deaths seems probable *a priori*, there is no way to demonstrate it directly. It is, however, possible to get some indirect evidence which will help towards the estimation of the extreme possible error which would be made if this assumption were wholly wrong.

The most marked evolutionary trend in table 2 is seen in the mortality charged against the alimentary tract and its associated organs. Now suppose we make the two possible assumptions which will set the extreme limits of the effect which could be produced by altering the distribution of the organologically unassignable deaths of Class X.

I. The first of these assumptions is that

$$\text{All X} = \text{VI},$$

that is, that all the deaths now in Class X were in fact due to breakdown of the alimentary tract and its associated organs.

This is obviously a biologically improbable assumption, but limiting assumptions often are highly improbable.

II. The second assumption is that

$$\text{No X} = \text{VI}$$

that is, that no death now in Class X was due to lesions of the alimentary tract or its associated organs. This again is a highly improbable assumption, but it is limiting.

The resultant effect of redistributing the proportionate mortality according to these two assumptions, together with the

TABLE 3

The proportionate mortality assigned to breakdown of the alimentary tract and its associated organs, under each of three assumptions

ANIMAL GROUP	ASSUMPTION I ALL X = VI	X IS RANDOM SAMPLE OF ALL DEATHS. (DATA FROM TABLE 2)	ASSUMPTION II NO X = VI
	per cent	*per cent*	*per cent*
Reptiles	77.6	58.6	31.7
Birds	63.5	50.83	37.8
Mammals	51.5	38.66	30.6
Man, São Paulo	43.3	39.22	36.9
Man, England and Wales	29.8	21.40	19.1

initial assumption of random distribution of the deaths in Class X, which underlies table 2, is shown in table 3.

In order to make clearer the significance of the data of table 3, figure 2 has been prepared.

It is seen that the trend of the mortality under Assumption II is, as a whole, slightly downward if man in England and Wales be taken into account. Leaving this last point out of consideration the trend under Assumption II is nearly horizontal. But under the limiting Assumption I the trend is plainly downward. The true facts must fall somewhere between I and II. Hence the conclusion seems to be that, however the unassignable mortality of Class X may be supposed to be distributed, there has been a steadily decreasing proportion of the total mortality due to breakdown of the alimentary tract during the evolutionary progression from reptiles to man.

The limiting assumptions were applied in the same way to the mortality from breakdown of the respiratory system, with

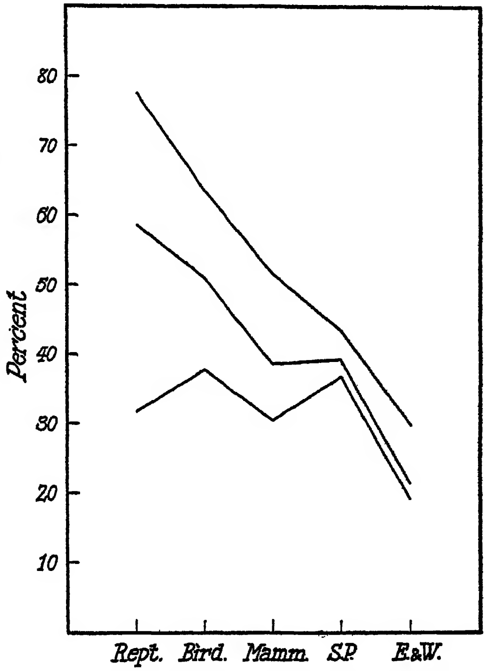


FIG. 2. TREND OF THE MORTALITY ASSIGNED TO CLASS VI, UNDER THREE ASSUMPTIONS

the similar result of showing that the evolutionary trend of the mortality assignable to this system has been, in greater or smaller degree, in the *direction* indicated in table 2.

It would seem, then, that even though the anatomically unassignable mortality in the London Zoological Garden material is absolutely larger than is desirable, still the element of uncertainty that is thereby introduced into our conclusions pertains

rather to the *rate* of the evolutionary changes in mortality, than to their *sense* or direction.

THE PRIMITIVE GERM LAYERS AND MORTALITY

One obvious advantage of the organological classification of mortality is that it permits the final grouping of deaths into three large classes, based upon the assignment of the different organs of the body to the primary germ layers from which they developed embryologically. There are, of course, difficulties in making as detailed and precise a distribution of the mortality of the lower animals to the primary germ layers as can be done with human mortality. But probably the final intrinsic errors are not really greater, because the greater accuracy of the diagnoses based on autopsies in the lower animals, as compared with the general vital statistics of human beings based merely upon the physicians' opinion as to the cause of death, probably offsets the other deficiencies in the material. In any case I think the results presented in table 4 may be regarded as at least an approximation to the true facts.

TABLE 4

The distribution among the three primary germ layers of each 100 organologically classified deaths

GERM LAYER	REPTILES	BIRDS	MAMMALS	MAN (SÃO PAULO 1917)	MAN (ENGLAND AND WALES, 1914)
Ectoderm.......	0.7	0.1	1.0	7.2	11.0
Mesoderm.......	7.7	11.6	13.5	28.0	35.2
Endoderm.......	91.6	88.3	85.5	64.8	53.8
Totals.......	100.0	100.0	100.0	100.0	100.0

The orderly character of the data in table 4 is striking. Proceeding up the evolutionary scale from the extreme left hand column of the table (Reptiles) to the extreme right hand column (Man in England) the proportionate mortality from breakdown of organs developing from the ectoderm, and from the mesoderm, *increases*, while the proportionate mortality associated with organs which develop from the endoderm *diminishes*.

These figures are shown graphically in figure 3.

DISCUSSION

In the initial discussion of the organological classification of mortality the following statement was made (10, pp. 168 and 169):

"Taking a general view of comparative anatomy and embryology it is evident that in the evolutionary history through which man and the higher vertebrates have passed it is the ectoderm which has been most widely differentiated from its primitive condition, to the vitality of which statement the central nervous system furnishes the most eloquent evidence. The endoderm has been least differentiated in the process of evolution, while the mesoderm occupies an intermediate position in this respect. An elaborate array of evidence might be presented on these points, but to do so would be supererogation. It would amount simply to repeating any standard treatise on the comparative anatomy of the vertebrates.

"From the present point of view we see that the germ layer, the endoderm, which has evolved or become differentiated least in the process of evolution is least able to meet successfully the vicissitudes of the environment. The ectoderm has changed most in the course of evolution. The process of differentiation which has produced the central nervous system of man had as a concomitant the differentiation of a protective mechanism, the skull and vertebral column, which very well keeps the delicate and highly organized central nervous system away from direct contact with the environment. The skin exhibits many differentiations of a highly adaptive nature to resist environmental difficulties. It is then not surprising that the organ systems developed from the ectoderm break down and lead to death less frequently than any other."

These inferences were drawn from an examination of the evidence from human

mortality alone. Now we have at hand in tables 2 and 4 of the present paper some additional evidence. We see at once that all along the evolutionary pathway, from reptiles to man, the endoderm has had the largest absolute mortality chargeable against it, but the *proportionate* amount has steadily diminished. It is a possible inference from the evidence that the organs derived from endoderm have become progressively better adapted to meeting successfully the environmental stresses and strains which bear upon them in the business of living.

On the other hand the proportionate mortality assignable to the organs derived from the ectoderm and the mesoderm has increased in the course of evolution. There is, of course, a necessary compensation in this. If 100 per cent of mortality is divided into parts and some of these parts exhibit a secular change, up or down, the other parts must of necessity show a trend in the opposite sense. If preventive medicine has in any degree reduced the *proportionate* number of deaths associated with the endodermal organs, just by so doing it must necessarily have increased the *proportionate* mortality associated with either ectodermal or mesodermal organs, or both. But it should not be overlooked that the same trends

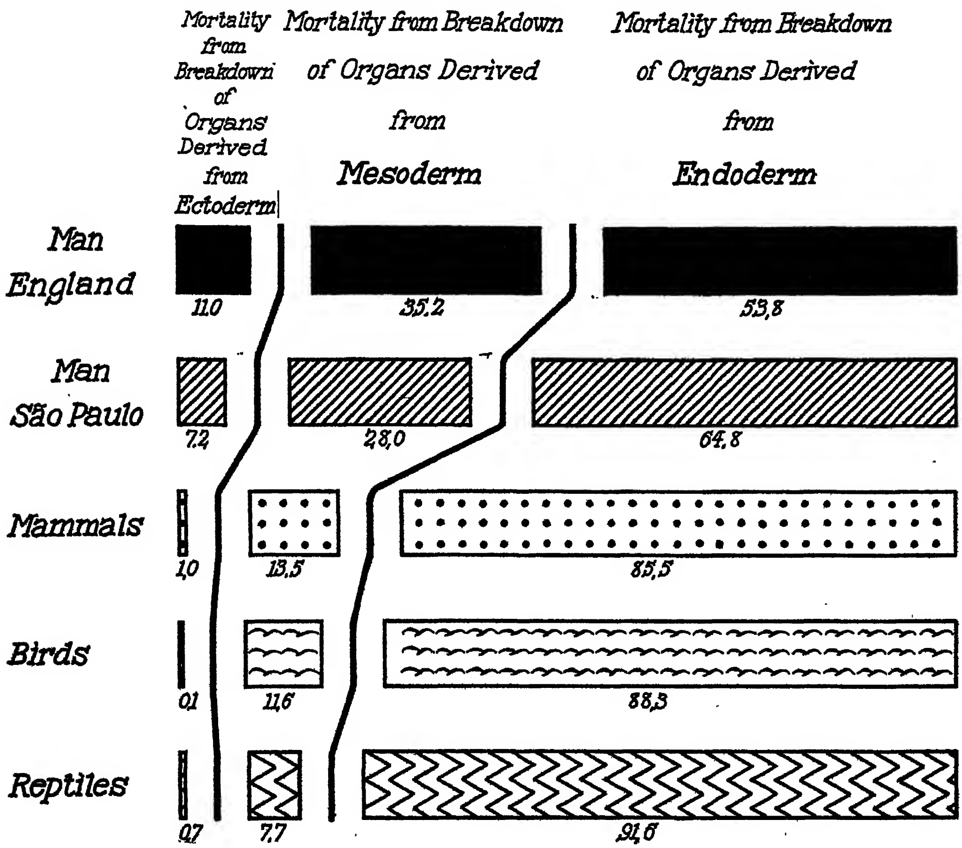


FIG. 3. THE MORTALITY, PER HUNDRED DEATHS FROM ALL CAUSES, DISTRIBUTED ACCORDING TO THE PRIMARY GERM LAYERS FROM WHICH THE DIFFERENT ORGAN SYSTEMS DEVELOP EMBRYOLOGICALLY

are observable in the proportionate mortalities of ecto, meso, and endodermal organs before man and preventive medicine are reached. So perhaps this art and science has only altered the course of evolutionary events quantitatively, and not qualitatively.

In conclusion I should like to say that no one can possibly recognize more clearly than I do the shortcomings of the data used in this discussion, including those for man as well as those for the lower animals. The results can at best be regarded only as suggestive, and not as probative. But, considered simply as description, they nevertheless do adumbrate another, and, so far as I know, new example of the "order of nature." It may be that the biological philosophy upon which the figures of mortality are here arranged is not the one of maximum heuristic value. But at least the system upon which the mortality data are here arranged is rational and consistent. No other system, actually in use, for classifying the pathologically recognized and statistically recorded causes of death can lay any claim to consistent rationality. The official "International List" for the classification of the causes of death shifts its basis, within its titles, with complete casualness and abandon between etiology, organology, embryology, and mere symptomatology. As was recently (1) pointed out in *The Lancet:* "The useful definition of a disease may be aetiological—e.g., typhoid fever—or anatomical—e.g., cirrhosis of liver—or purely symptomatic—e.g., epilepsy; all such criteria are, in the final sense, provisional, but they do very well in practice." So they do. But from the viewpoint of logical classification of all mortality nothing is gained by mixing these different bases in the same classificatory scheme.

The further the present rational and consistent system of studying comprehensively the biology of human mortality is carried, and we have accumulated a large amount of work in this direction as yet unpublished, the more does it appear to justify itself as a method of research on an extraordinarily complex and difficult problem of biology. No further claim on its behalf need be made at this time.

LIST OF LITERATURE

1. Anonymous. Nomenclature. The Lancet, January 28, 1928, pp. 194–195.
2. Fox, H. Disease in Captive Wild Mammals and Birds. Incidence, Description, Comparison. With a Foreword by Charles B. Penrose, M.D. Philadelphia (J. B. Lippincott Co.). No date (Copyrighted 1923). Pp. vii + 665 + 3 unnumbered.
3. Laycock, T. Clinical lectures on the physiognomical diagnosis of disease. Delivered at the Royal Infirmary, Edinburgh. Med. Times and Gaz., Vol. I for 1862, pp. 1–3; 51–54; 101–103; 151–154; 205–208; 287–289; 341–344; 449–451; 499–502; 551–554; 635–637.
4. Lucas, N. S. Report on deaths which occurred in the Zoological Gardens during 1920. Proc. Zool. Soc. London, 1921, pp. 179–182.
5. Lucas, N. S. Report, etc., during 1921. *Ibid.*, 1922, pp. 281–283.
6. ———. Report, etc., during 1922. *Ibid.*, 1923, pp. 125–128.
7. ———. Report, etc., during 1923. *Ibid.*, 1924, pp. 293–296.
8. Pearl, R. Certain evolutionary aspects of human mortality rates. Amer. Nat., Vol. 54, pp. 5–44, 1920.
9. ———. The Biology of Death. Philadelphia (Lippincott), 1922. Pp. 275.
10. ———. Studies in Human Biology. Baltimore (Williams & Wilkins Co.), 1924. Pp. 653.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that The Quarterly Review of Biology *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* The Quarterly Review of Biology, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

ABSTAMMUNGSLEHRE UND NEUERE BIOLOGIE.
By Richard Hertwig. *Gustav Fischer*
14 marks 7 x 10; 271 (paper) *Jena*
(Bound 16 marks)

In this volume a great master of zoology reviews Darwinism, and critically evaluates its present position in the light of the new biological knowledge which has accrued during the enormously active and fertile years of the twentieth century, particularly in the field of genetics. The book has three main divisions. The first of these is chiefly historical, concerning itself with the development of the theory of evolution. The second, and longest, section is a critical review of modern genetics and its bearing upon the theory of evolution. The last section of the book is concerned with phylogeny, chiefly from the viewpoint of critically considering the kinds of evidence which will lead to sound knowledge in this field. Altogether it is a stimulating and valuable contribution, the usefulness of which to the student is unfortunately diminished by the fact that it contains no bibliographical documentation whatever.

LA DESCENDANCE. *L'hérédité. L'origine des caractères. La fécondation. La vieillesse.*
By Pierre-Jean. *Félix Alcan*
15 francs $5\frac{5}{8}$ x 9; 238 (paper) *Paris*

A philosophical discussion of life and evolution, from the viewpoint of a psychologist, whose position is that consciousness (and its derivative, memory) is an indispensible and irreducible element of all life, alone capable of explaining the observed facts of adaptation. An interesting book.

DEVELOPMENT AND PURPOSE. *An Essay Towards a Philosophy of Evolution.*
By L. T. Hobhouse. *The Macmillan Co.*
$6.00 $5\frac{1}{2}$ x $8\frac{1}{2}$; xxxix + 494 *New York*

A thoroughly revised, indeed largely rewritten, edition of a book that has long been a classic of modern philosophy. The general conclusion is unchanged, that the world process is "a development of organic harmony through the extension of control by Mind operating under mechanical conditions which it comes by degrees to master. The empirical synthesis is in the main limited to the history of mind upon this earth, and to the stages by

which intelligence makes for itself a vehicle in the physical organism. The deductive argument exhibits this process as a part of a vaster and more significant evolution. But the strength of the position is that, so far as the two arguments cover the same ground, they coincide in the main lines of their teaching."

TRAVELS IN SPAIN AND THE EAST. *1808–1810.*
By Sir Francis Sacheverell Darwin.
The Macmillan Co.
$2.40 5 x 7½; ix + 121 *New York*

Sir Francis Sacheverell Darwin was the sixth son of Erasmus Darwin. In 1808 he set out from Birmingham to see the world with Mr. Theo. Galton, Francis Galton's uncle, and three other companions. This book is his diary for the next two years. It is delightful reading. They had plenty of adventures, and saw a great many interesting things in a trip which took them as far east as Constantinople. Of the original party one is robbed and murdered on the road, soon after they land in Spain; a second goes to the bottom in the Viper between Cadiz and Gibraltar; a third joins the army and is killed on the retreat to Corunna. Finally Mr. Galton gets the plague in Malta and dies, Mr. Darwin staying with him to the end.

The book is a welcome addition to Darwiniana and Galtoniana.

GENETICS

THE GENETICS OF SEXUALITY IN ANIMALS.
By F. A. E. Crew. *The Macmillan Co.*
$4.00 5½ x 8½; + 188 *New York*

This book, which is published in the *Cambridge Comparative Physiology* series covers, in greater detail, similar ground to that reviewed in The Quarterly Review of Biology in the articles by Professor Crew which appeared last year. The material is discussed under the following heads: The mechanism of sex-determination; the physiology of sexual differentiation; sex-reversal in the adult individual; the mode of inheritance of sex-dimorphic characters; and the sex-ratio. There are very extensive and complete bibliographies. The book will be extremely valuable as a reference source for the development of knowledge up to the present time in what is just now one of the most lively fields of biological research.

THE HARVEST OF THE YEARS.
By Luther Burbank with Wilbur Hall.
Houghton Mifflin Co.
$4.00 5½ x 8; xxvi + 296 *Boston*

Essentially an autobiography of an interesting human being, though largely written in actual fact by Mr. Hall after Mr. Burbank's death, but with the aid of copious notes which he had left. Every student of genetics will be interested in reading this volume, particularly between the lines. It is illustrated with some twenty odd photographs, chiefly portraits of Mr. Burbank and his friends. The book is a fine record of a useful life. It lacks an index.

A RÉSUMÉ OF CATTLE INHERITANCE.
By John W. Gowen. *Martinus Nijhoff*
2.60 guilders *The Hague*
6¼ x 9¾; 54 (paper)

A thorough review, with a bibliography of 156 titles, of the present state of knowledge regarding inheritance in domestic

cattle. The genetics of more than thirty characters has been studied. Dr. Gowen's own outstanding work in this field makes him the person of choice to do such a comprehensive and critical review as this.

GENETICS OF DOMESTIC CATS.
By Ruth C. Bamber (Mrs. Bisbee). *Martinus Nijhoff*
4.40 guilders *The Hague*
$6\frac{1}{4}$ x $9\frac{3}{4}$; 86 (paper)

The domestic cat has furnished some entertaining genetic puzzles. It is a valuable service which Mrs. Bisbee has performed in bringing together and critically reviewing all the scattered literature in the field. She says that the problem of the tortoise-shell male "is by no means settled."

MENDELISM.
By Reginald C. Punnett. *The Macmillan Co.*
\$3.00 $4\frac{7}{8}$ x $7\frac{5}{8}$; xv + 236 *New York*

The seventh edition of one of the earliest and best popular expositions of the principles of Mendelian inheritance. The chief alterations in the revision relate to Goldschmidt's work on intersexes, and the chromosome theory of genetic phenomena.

GENETISCHE ANALYSE VAN KLEUREN, VEERPATRONEN, TINTEN EN AFTEEKENINGEN BIJ POSTDUIVEN.
By C. J. A. C. Bol. *Martinus Nijhoff*
5 guilders *The Hague*
$6\frac{5}{8}$ x $9\frac{7}{8}$; 108 (paper)

A detailed account of an investigation of the genetics of color and pattern in the plumage of carrier pigeons. There is a bibliography of twenty titles.

GENERAL BIOLOGY

AUS DEM LEBEN DER BIENEN.
By K. v. Frisch. *Julius Springer*
4.20 marks $4\frac{5}{8}$ x $7\frac{1}{4}$; x + 149 *Berlin*

DIE LEHRE VON DER VERERBUNG.
By Richard Goldschmidt. *Julius Springer*
4.80 marks $4\frac{5}{8}$ x $7\frac{1}{4}$; vi + 217 *Berlin*

EINFÜHRUNG IN DIE WISSENSCHAFT VOM LEBEN ODER ASCARIS. *2 vols.*
By Richard Goldschmidt. *Julius Springer*
8.80 marks for 2 vols. *Berlin*
$4\frac{5}{8}$ x $7\frac{1}{4}$; xi + 340

The first three numbers in a new series of popular scientific treatises, having the general title *Verständliche Wissenschaft.* The books are very attractively printed and bound, abundantly and well illustrated. So far as one may judge from the first numbers, the intrinsic merits of the series would seem to warrant the prediction of a considerable success for it.

The first volume gives the best account of the biology of the honey bee that we have seen in equal space. A great deal of attention is devoted to the experimental work which has been done on the behavior of the bee.

The first of the volumes by Professor Goldschmidt is an exposition of the present state of knowledge of genetics. The second, in two volumes, is a wide-ranging discussion of adaptation in the animal world. Both are extremely well done. The latter appeals to us especially as a fine piece of literary work, calculated to excite the interest and hold the attention of the general reader, to a degree rarely attained in popular scientific writing.

ANIMAL ECOLOGY.
By Charles Elton. *The Macmillan Co.*
\$4.00 $5\frac{1}{2}$ x $8\frac{1}{2}$; xx + 207 *New York*

An interesting and original treatise on ecology, which from the author's point of

view "simply means scientific natural history." This attitude towards the subject is in refreshing contrast to that of some American workers in this field, who, in their zeal to be up-to-date and strictly in the mode, appear to regard ecology as a branch of physics. Mr. Elton discusses the subject under the following heads: The distribution of animal communities; ecological succession; environmental factors; the animal community; parasites; time and animal communities; the numbers of animals; variations in the numbers of animals; dispersal; ecological methods; ecology and evolution. There is a bibliography of 152 titles on the general subject, and a number of specific references to systematic works on British animals. Altogether this is a valuable contribution to the literature of general biology.

Professor Julian Huxley contributes an introduction.

LEBEN. ALTERN. TOD.
By E. Korschelt, S. Hirsch, F. W. Harms, M. Hartmann and H. Driesch.
Hugo Bermühler
2.50 marks *Berlin-Lichterfelde*
7 x 10; 81 (paper)

A collection of five lectures, by the authors named, given in Frankfurt in 1925–26. Prof. Korschelt deals with duration of life in animals and plants; Dr. Hirsch with the phenomenon of senescence and death; Dr. Harms with rejuvenation and the prolongation of life; Dr. Hartmann with death, reproduction and rejuvenation, with special reference to the protozoa; and finally Prof. Driesch with life, death and immortality. The treatment is in all cases popular in style. There is no index.

HIPPOKRATES. *Eine Auslese seiner Gedanken über den gesunden und kranken Menschen und über die Heilkunst.*
By Arnold Sack. *Julius Springer*
4.50 marks *Berlin*
$5\frac{1}{2}$ x $8\frac{1}{2}$; 87 (paper)

A selection of quotations from the writings of Hippocrates, translated into German and assembled under 29 heads. The choice of material is excellent. While primarily intended for medical students, the general biologist will find much of interest in the book, and except in such a form he is not likely to read Hippocrates at all.

LIVING CREATURES. *Studies of Animal and Plant Life.*
By C. von Wyss. *A. and C. Black, Ltd.*
12s. 6d. net *London*
$5\frac{1}{2}$ x $8\frac{1}{2}$; xi + 406

An excellent "nature study" book, by a successful teacher of "Natural History in the wide sense." There are 27 chapters, of which 21 deal with common animal forms, chiefly insects, while the remaining chapters are devoted to plant topics. The book is well written; and, as Prof. J. Arthur Thomson says in his Foreword, "gives us glimpses of the Drama of Life." There is an index.

EXPERIMENTAL EMBRYOLOGY.
By Thomas H. Morgan.
Columbia University Press
$7.50 $5\frac{7}{8}$ x $9\frac{1}{8}$; xi + 766 *New York*

In a later number of The Quarterly Review of Biology this important volume will receive extended notice.

HUMAN BIOLOGY

SYMBOLISM. *Its Meaning and Effect.* *By Alfred North Whitehead.*

The Macmillan Co.

$1.50 $5 \times 7\frac{5}{8}$; x + 88 *New York*

This small volume includes three lectures given at the University of Virginia, under the Barbour-Page Foundation. At the start we are given this definition:

> The human mind is functioning symbolically when some components of its experience elicit consciousness, beliefs, emotions, and usages, respecting other components of its experience. The former set of components are the "symbols" and the latter set constitute the "meaning" of the symbols. The organic functioning whereby there is transition from the symbol to the meaning will be called "symbolic reference."

The author then develops the significance and consequences, philosophical and social, of this kind of mental activity.

> It is the first step in sociological wisdom, to recognize that the major advances in civilization are processes which all but wreck the societies in which they occur:—like unto an arrow in the hand of a child. The art of free society consists first in the maintenance of the symbolic code; and secondly in fearlessness of revision, to secure that the code serves those purposes which satisfy an enlightened reason. Those societies which cannot combine reverence to their symbols with freedom of revision, must ultimately decay either from anarchy, or from the slow atrophy of a life stifled by useless shadows.

ENVIRONMENT AND RACE. *A Study of the Evolution, Migration, Settlement and Status of the Races of Man.*

By Griffith Taylor. *Oxford University Press*

$7.50 $5\frac{1}{2} \times 8\frac{1}{2}$; xv + 354 *New York*

This is a study of the population problem along anthropological lines, by the head of the Department of Geography in the University of Sydney. The book starts with the thesis that "the world problem of today is the adjustment of the nations to the crowding which for the first time in history is affecting the whole earth." The discussion of this, and various subsidiary problems which arise from it, is divided into four parts. The first is introductory, stating the problem and the technique to be used in its discussion. The second part deals with "The Changing Environment and Race Distribution," in the past. It is a comprehensive review of the author's views as to the forces which have influenced migration. The third part is devoted to a discussion of the white race in the Australian environment at the present time. Finally, the fourth part of the book is given to a prophesy as to the future distribution of the white race. The conclusion reached is embodied in the following table:

Future white settlement and its political control

	BRITISH	U. S. A.	OTHER STATES	TOTAL
	millions	*millions*	*millions*	*millions*
I. North American region (52 per cent of total) ...	179	513	10	702
II. European region (29 per cent of total)..........	60	...	326	386
III. Argentine region (8.5 per cent of total)..........	...	...	115	115
IV. South African region (6 per cent of total)........	76	...	6	82
V. Australian region (4.5 per cent of total)	62	...	...	62
Total..............	377	513	457	1,347
Percentage..........	28	39	33	100

Whether one agrees with all the author's conclusions or not this is an extremely interesting and provocative book.

ORGANIC INHERITANCE IN MAN.
By F. A. E. Crew. *Oliver and Boyd*
12s. 6d. *Edinburgh*
$5\frac{1}{2} \times 8\frac{3}{4}$; xxviii + 214

This volume embodies the subject matter of a series of lectures to the medical profession of Birmingham, given by the distinguished Director of the Animal Breeding Research Department of the University of Edinburgh, as the first course under the William Withering Memorial. In the publication of the lectures the author has deemed it reasonable "to avoid any strenuous effect to observe meticulous accuracy and elaborate detail, but rather to attempt to give an intelligible presentation of principle. Authorities, though abundantly quoted, are not named, and there is no bibliography."

Professor Crew presents in this volume one of the best accounts that we have ever seen, for the intelligent reader not specially trained in biology, of the basic principles of genetics, on the one hand, and of the known facts of human inheritance, on the other hand. Being at once a master in the field of genetics and a medical man, he is peculiarly fitted for such a task. The last chapter of the book is entitled "Concerning the Implications of Genetic Fact and Theory." In its eight pages is embodied a splendid statement of a sound eugenic position, with a minimum of the preaching usually found in eugenical writings. We like particularly the following paragraph:

> But who shall sit in judgment and separate fit from unfit? These are relative terms, and in their definition one must allow for differences in point of view. Before action is taken, it is essential that man shall know what is man and what man may become. If and when it is decided what kind of thing mankind shall become, if and when standards of merit have been constructed, then the biologist will be able to help in the achievement of these by indicating the most promising methods of approach. But the biologist alone is not competent to draw up these standards: neither is the enthusiastic amateur statesman whose only claim to note is his sincerity.

An appendix carries some 50 odd pedigree charts showing the familial incidence and mode of inheritance of various human characteristics, particularly diseases.

HUMAN STERILIZATION.
By Rev. John A. Ryan.
National Catholic Welfare Conference
Washington, D. C.
$5\frac{3}{8} \times 8\frac{1}{4}$; 10 (paper)

Father Ryan, who is an acute person, starts by quoting from André Siegfried's *America Comes of Age*, and then says:

> Once men reject the truth that the human person is intrinsically sacred, that even his body should be treated with reverence, they can easily persuade themselves that any person may be used in any fashion for the benefit of society. The difference between the social inconveniences arising from the existence of too many imbeciles and that resulting from the presence of too many Negroes, Mexicans or other non-Nordics, is a difference only of degree—possibly in favor of the imbeciles. If sterilization is no degradation of personality, no violation of natural rights, why should it not be applied to all the inferior classes that bring more inconvenience than convenience to the politically dominant *élite*?

The question seems to us a hard one to answer, but then rhetorical questions often are difficult to deal with adequately. In fact that seems to be one of the main reasons why people ask them.

Dr. H. H. Laughlin's "model eugenical sterilization law" is discussed, and it is pointed out that in that potential statute a "socially inadequate person" is defined as one who, along with other sad stigmata, "fails chronically in comparison with normal persons to maintain himself or herself as a useful member of the organized social life of the State."

We agree with Father Ryan that this is

a bit too inclusive. Furthermore it seems prolix. Why not define a socially inadequate person as one who "is disapproved of by Mr. A, or Mr. B, or Mr. C?" Or, if anyone of these, being a modest man, dislikes the publicity this would involve, substitute for his name that of the Hot Water Haven and World Eugenic Society, or the Ku Klux Klan, or the Anti-Saloon League? They all labor for noble causes and dislike objectionable people.

THE BUILDERS OF AMERICA.
By Ellsworth Huntington and Leon F. Whitney. *William Morrow and Co.*
$3.50 $5\frac{3}{4} \times 8\frac{3}{4}$; xiv + 368 *New York*

A contribution to eugenic evangelism dedicated to Irving Fisher, and ending on the following high note:

> Positive eugenics will increase the rarer, lovelier blossoms in the Queen's garden, and improve the commoner ones. It will restore to the garden the borders and beds of beautiful pansies like unto the black velvet gown of a bishop, the yellow silk of a duchess, the royal purple of a king, the motley of the gayest of clowns, and the white robe of a bride. It will do far more than this, for when the Queen's garden has enough seed of these rare kinds, and when sufficient seed is carefully preserved, lo, here and there, and then all over the broad land even the little flower beds of the peasants will be bright with blossoms like those in the Queen's own garden.

The book contains a large amount of interesting statistical material, some of which is new, bearing directly or indirectly upon eugenic problems.

PRIMITIVE MAN. *His Essential Quest.*
By John Murphy. *Oxford University Press*
$5.00 $5\frac{1}{2} \times 9$; xiv + 341 *New York*

This is a comprehensive and intelligent attempt to discuss the psychological evolution of human kind, and to evaluate the significance of mind as a factor in evolution in general. The point of view of the whole study is indicated by the following quotation:

> The process of integration through differentiation, which is the method of the creative evolution of the universe, takes conscious form in man. It expresses itself in man's essential quest, which is directed towards the unification of his life. In this quest for unity within himself, he is seeking always a deeper and more sensitive integration, together with the utmost possible variety of differentiation. The imperfection of the instruments with which he works at the earlier stages of his human evolution—in particular, his imperfectly coördinated brain and mind—accounts for the imperfection of his earlier attempted unifications, and the manifold forms of his theories and customs. The integration of man's inner life involves certain integrations of his environment, of his world, including his fellows and his societies, unifications of himself with his world and of his world with himself.

There is a brief, but well chosen bibliography.

A SHORT HISTORY OF WOMEN.
By John Langdon-Davies. *The Viking Press*
$3.00 $5\frac{3}{4} \times 8\frac{1}{4}$; xiv + 382 *New York*

A most interesting book, which has been in the "best seller" class. The central thesis of the book, supported by much entertaining material derived from anthropological literature and the author's own observations, is that the history of women is the

> history of human ideas about the nature and differences of the two sexes; and as we have followed it, these ideas have consistently been based upon the same mistaken notions about biology. The primitive savage, the primitive Christian, the feudal knight, the seventeenth-century Puritan, the eighteenth-century essayist, the Victorian drawing-room tea-drinker; all alike thought and acted about women as they did because the same superstitions about biology and the same misinterpretation of feelings were common to all. The dawn came when people began to suggest that women were quite as

reasonable by nature as men, and that wrong education was responsible for any difference between them in this respect. After that came political emancipation and economic emancipation, until today we can say that the first is complete and the second almost as far advanced as it is for individuals of the male sex.

Not being a pedant or a professor the author is not afraid to write with some wit and humor.

THE MEINI HIRION AND SARNS OF ANGLESEY (*Considered in relation to the early Hundred System*). *A Key to the Antiquities of Britain.*
By William Evans *William Evans*
2s. 9d.
Pen-y-Bont, Red Wharf Bay, Anglesey
$5\frac{1}{4} \times 8\frac{1}{4}$; 49

"Meini Hirion" are menhirs. This book is a concise account of an investigation which must have cost the author a great deal of time and labor. The conclusion is that these stone monuments were boundary stones marking roads which divided the island into blocks of sixteen square miles each. Each square mile is supposed to be a township. Giraldus Cambrensis, who lived while the ancient "Hundred System" was still followed in Wales, says that Anglesey was divided into three Hundreds, made up of 343 townships or *trefydd.* There are in fact 343 plots of one square mile each on the island after allowing for roads and public spaces. There is thus evidence in favor of Mr. Evans' theory.

SOCIALITY. *The Art of Living Together.*
By Atkinson Lee. *Holburn Publishing House*
5 shillings $5 \times 7\frac{1}{2}$; xxvi + 305 *London*

This book is more in the tone of a somewhat pallid Unitarian tract than a scientific treatise. The general idea is that social living is not "either a science or a duty, but an act." The attempt is made to measure social values in terms of aesthetics. It is held that only in the religious realm can full sociality be realized. The book abounds in beautifully turned phrases, and should prove a veritable boon to parsons hard up for sermon material. The biologist will find it less useful.

THE NATURAL HISTORY OF A SAVANT.
By Charles Richet. Translated from the French by Sir Oliver Lodge. *George H. Doran Co.*
$2.00 net $5 \times 7\frac{1}{2}$; xi + 155 *New York*

This translation of a most entertaining book, which every scientific man should read, and particularly the beginner in science, is extremely well done. It preserves well the charm of the original. The natural history of great men is a branch of human biology too much neglected. While Richet's little book was written primarily for fun, both his and the reader's, it contains much real wisdom, and some brief sketches of really great men, which in their delicacy and sharpness of detail remind one of the engravings of the Little Masters.

THE RACIAL CHARACTERS OF THE SWEDISH NATION.
Edited by H. Lundborg and F. J. Linders.
The Swedish State Institute for Race Biology
100 Swedish crowns *Uppsala*
(*American distributor G. E. Stechert and Co.*, N. Y.)
$11\frac{1}{4} \times 15$; xiv + 108 + 44 plates
(paper)

A magnificent contribution to physical anthropology and eugenics, the result of

coöperative effort, ably guided by the distinguished Director of the *Swedish State Institute for Race Biology*. Following a brief historical section comes the first part of the main work, which includes seven chapters on the general anthropology and demography of the Swedish people. The second and largest section of the work is devoted to the exhibition and analysis of extensive series of anthropometric measurements. The final main section is devoted to the results of certain special investigations, bearing upon the main theme. At the end are 44 plates of beautifully reproduced photographs of Swedish types. No student of human biology can do without this book.

THE SURVIVAL OF THE UNFITTEST.
By Charles Wicksteed Armstrong.

The C. W. Daniel Co.
6 shillings net $4\frac{3}{4} \times 7\frac{1}{4}$; 160 *London*

An entertaining and forceful contribution to eugenic discussion. The book presents arguments in opposition to about all forms of social uplift—particularly organized charity—except eugenics and, by inference, birth control. Eugenic doctrines are presented as the solution of most of our troubles, and in one chapter, called "A Fascinating Scheme," a plan for a Eugenic Settlement is worked out in detail.

HUMAN ENVIRONMENT AND PROGRESS. *The Outline of World Historical Geography.*
By W. R. Kermack.

W. and A. K. Johnston
4 shillings *Edinburgh*
$4\frac{7}{8} \times 7\frac{1}{4}$; viii + 231

This little book is developed in three sections. The first lays down the principles of historical geography, which amounts to human ecology historically treated. The second section, which comprises somewhat more than half the book, deals with the British Empire and the United States. The final section is devoted to the rest of the world. The treatment is highly condensed. Perhaps partly because of the condensation, there are some careless slips in details. But on the whole it is a readable, interesting, and informative book, well illustrated, but unfortunately lacking an index.

THE EARLY HISTORY OF MAN. *With Special Reference to the Cap-Blanc Skeleton. Anthropology Leaflet 26.*
By Henry Field.

Field Museum of Natural History
25 cents $5\frac{1}{2} \times 8\frac{1}{2}$; 15 + 8 plates *Chicago*

The rock sculpture at Cap Blanc, near Moustier, is one of the great sights of the world. Few things can give the person, sufficiently intelligent to grasp its significance as a document in the history of human kind, a greater thrill than this frieze of horses, sculptured in high relief on the cliff face, with an artistry that has rarely been equalled. The little booklet from the Field Museum tells the story of this prehistoric station briefly, but extremely well, and with adequate illustrations.

ANCIENT CIVILIZATIONS. *From the Earliest Times to the Birth of Christ.*
By Donald A. Mackenzie.

Blackie and Son, Ltd.
12s. 6d. $5\frac{5}{8} \times 8\frac{1}{4}$; xix + 283 *London*

This volume deals with the ancient empires of Egypt, Asia, and Southeastern Europe from the earliest times of which

there is record down to the birth of Christ. Special attention is given to origins and to attempts to connect history with prehistory. The book is abundantly illustrated with excellent photographs, and will be found useful to the reader who wishes to get, in brief space, a reasonable knowledge of the beginnings of human history.

HEALTHY GROWTH. *A Study of the Relation Between the Mental and Physical Development of Adolescent Boys in a Public Day School.*
By Alfred A. Mumford.
Oxford University Press
$5.00 *New York*
$5\frac{3}{8}$ x $8\frac{1}{4}$; xxiii + 348

A well-written account of the growth and physiology of English schoolboys. Substantially all the thorough, careful observations made point towards the establishment of a positive relationship between mental and physical growth. Scholars, compared with non-scholars, are superior in respect of the condition of the mucous membrane of nose and throat; they have better vision, and teeth with less tendency to decay. The book is packed with interesting observations and is an important contribution to the literature of child hygiene and public health in general, as well as to physical anthropology.

FIGHTERS OF FATE. *A Story of Men and Women Who Have Achieved Greatly Despite the Handicaps of the Great White Plague.*
By J. Arthur Myers.
The Williams & Wilkins Co.
$3.00 $5\frac{3}{8}$ x $7\frac{1}{2}$; xix + 318 *Baltimore*

Brief biographies of 23 men and one woman who had, or have, tuberculosis and have attained fame, in greater or less degree, by their achievements in one or another field of human endeavor. The sketches are entertainingly written, and the whole forms an interesting contribution to the literature of human biology. Dr. Charles H. Mayo contributes an introduction. The book is beautifully printed and bound.

IMMIGRATION CROSSROADS.
By Constantine Panunzio.
The Macmillan Co.
$2.50 $5\frac{1}{4}$ x $7\frac{3}{8}$; ix + 307 *New York*

A welcome addition to the literature of immigration. The author brings cogent, penetrating, and well deserved criticism of the existing immigration law of this country. He pleads for a consideration of the whole subject from an international point of view, and for a selection of immigrants based upon sound tests of individual worth, rather than the indiscriminating and ruthless exclusion of good and bad alike, if they happen not to be Nordics.

DIE GRUNDLAGEN DER CHINESISCHEN EHE. *Eine historisch-ethnographische Studie auf Grund des Gesetzbuchs der T'ang-Dynastie und Mandschu-Dynastie sowie ausgewählter klassischer und philosophischer Literatur.*
By Erich Schmitt. *F. A. Brockhaus*
14 marks 6 x 9; 223 (paper) *Leipzig*

An interesting and valuable contribution to the literature of human biology. The author, who is *Privatdozent* in the University of Berlin, has combed the classical, philosophical, and legal literature of China for material regarding marriage. The book is thoroughly documented, and

will serve as a useful reference source for occidental students.

DATEN UND TABELLEN FÜR DEN PRAKTIKER.

By H. von Hoesslin. *Georg Thieme*
3.25 marks 4 x 6¾; 98 (paper) *Leipzig*

A useful little compilation of numerical data of interest primarily to medical men, but also to physiologists, anatomists, and students of human biology generally. The range of facts presented is wide. Every biologist will find this volume worth a great deal more than it costs as a handy reference source.

IMMIGRATION RESTRICTION. *A Study of the Opposition to and Regulation of Immigration into the United States.*

By Roy L. Garis. *The Macmillan Co.*
$4.00 5½ x 8½; xv + 376 *New York*

A heavily documented review of the immigration legislation of the United States, which will be useful as a reference work. The book is introduced by a Foreword by Mr. Albert Johnson, chairman of the House committee on immigration and naturalization.

GUIDE TO PHYSICAL ANTHROPOMETRY AND ANTHROPOSCOPY.

By Chas. B. Davenport.
Eugenics Research Assoc.
75 cents *Cold Spring Harbor, N. Y.*
4 x 6¾; 53

A useful little handbook of instruction in anthropometric technique, primarily intended for the eugenic field worker. It constitutes the first number of a series contemplated by the Eugenics Research Association.

ZOOLOGY

DE LINNÉ À JUSSIEU: *Méthodes de la Classification et Idée de Série en Botanique et en Zoologie (1740–1790).*

By Henri Daudin. *Félix Alcan*
25 francs *Paris*
5½ x 8⅞; ii + 264 (paper)

CUVIER ET LAMARCK: *Les Classes Zoologiques et l'Idée de Série Animale (1790–1830).*

By Henri Daudin. *Félix Alcan*
60 francs *Paris*
5½ x 8⅞; Vol. I, xiii + 460 (paper)
Vol. II, 338 (paper)

The history of the theory and practice of taxonomic classification is, in a very considerable sense, the history of zoology as a whole. These three volumes by Dr. Daudin can only be regarded as a masterly accomplishment of an extremely difficult task. They constitute a contribution of first importance to the literature of the history of science.

Because of the magnitude and difficulty of the task the author has wisely set certain limitations upon his work. The first and most important is that he leaves to one side the question of genera and species and confines his attention to phyla. He shows how the supposedly continuous series—the *Scala naturae*—which was in the mind of the earlier taxonomists, came to be replaced by the great independent natural groups which today we regard as constituting the animal kingdom.

Another limitation is that, in the later period, he confines his attention largely to the French work. This however is justified because in the period of which he was writing France was the center of the zoological world. Cuvier and Lamarck were the great figures, with Etienne Geoffroy St. Hilaire, Latreille, Savigny, de Blainville, and Serres as the stars of lesser relative magnitude, but still of great absolute brightness.

The volumes are abundantly documented bibliographically.

BIRDS AND BEASTS OF THE GREEK ANTHOLOGY.
By Norman Douglas.
Obtainable from Norman Douglas, c/o T. Cook and Son,
$6.00 5½ x 8½; 219 *Florence, Italy*

This delightful and charming volume, privately and beautifully printed in an edition of five hundred numbered and signed copies, is the kind of book to be written under conditions which can only fill with envy and longing the heart of the poor devil tied to a dingy laboratory on a raw March day. Let the author tell about it.

Books have been written on the Natural History of the Bible, on that of Shakespeare, of Homer, Virgil and so forth: why not a similar one on the fauna of the Greek Anthology—though the flora, perhaps would be even more interesting? So I often thought, while reading and re-reading this marvellous collection which has been my companion for many months past. Three years, I finally concluded, might suffice for the venture. Three years, under some vine-wreathed arbour, with the necessary books at one's elbow, and one's soul at ease. Such a thing, it is obvious, should be a holiday performance; written *con amore* and not otherwise; in reverential, playfully-erudite fashion. Three years or even more; for I soon realized that the enterprise might well blossom—why not?—into a general treatise on ancient Natural History and the changes in animal economy which have occurred in the interval between then and now; that it would open up, incidentally, a number of questions social, aesthetic, and humanitarian, showing how the attitude of mankind towards birds and beasts has altered since those days. Three years, I kept on saying to myself—where shall they be found?

I shall not find them.

Be that a pretext for putting together the following notes which may serve as material for some one more fortunately situated. The pencillings then scrawled in my Anthology are fast fading; I amplified them later with references to such authorities as were accessible, but a good many others would have to be consulted if the undertaking were to be brought up to date, such as, for instance, von der Mühle's book on the Birds of Greece, which I have not been able to procure.

An undertaking, for the rest, of the gentlemanly kind; quite useless.

So it is throughout, just utterly useless, perfectly delightful literary gossip about birds and beasts, good food, and such like things. Perhaps the most important thing in the volume is the author's recipe for cooking a *langouste*.

A NATURALIST AT THE DINNER TABLE.
By E. G. Boulenger.
Gerald Duckworth and Co., Ltd.
6 shillings 5 x 7½; 160 *London*

A pleasantly and authoritatively written contribution to the ancillary literature of gastronomy. It is not a cookbook, but aims to inform the *bon vivant* about the natural history of many of the things which come to his plate. No epicure will fail to add this entertaining little volume to his library.

REALITIES OF BIRD LIFE. *Being Extracts from the Diaries of a Life-loving Naturalist.*
By Edmund Selous. Constable and Co., Ltd.
14 shillings *London*
5½ x 8¾; xvi + 351

A highly interesting contribution to natural history. It is a detailed record of field notes made in connection with "the intensive watching of birds in natural surroundings." A wide range of species is covered. Especial attention is given to courtship, mating, and nesting behavior. In the case of the ruff (*Pavoncella pugnax*) Mr. Selous' observations demonstrate sexual selection in the classic Darwinian

sense; the female, in three particular cases, having perfect freedom of choice among many suitors, chose exceptionally handsome and brilliant mates. Besides its value as a scientific record the book has great literary charm.

Professor Julian Huxley contributes an introduction.

THE BIOLOGY OF THE FROG.
By Samuel J. Holmes. *The Macmillan Co.*
$2.75 $5 \times 7\frac{3}{8}$; ix + 386 *New York*

The fourth, thoroughly revised edition of a standard elementary text in zoology. The revision has been mainly in the physiological sections of the book.

ZOOLOGY OF COLORADO.
By Theodore D. A. Cockerell.
University of Colorado
$2.00 6×9; vii + 262 *Boulder*

A semi-popular systematic account of the fauna of Colorado, with the bulk of the space devoted to mammals, birds, and insects. The book should be extremely useful in aiding the non-professional person to identify the common animals of the region. It is one of the Semi-Centennial Publications of the University of Colorado.

THE FUR-TRADE OF CANADA.
By H. A. Innis.
University of Toronto Library
$2.00 6×9; 172 *Toronto*

This is the first of a projected series of studies of the principal industries of Canada, made under the aegis of the Department of Political Science of Toronto University. While primarily economic in its outlook, it contains a great deal of information of interest and value to the ecologist.

A CONTRIBUTION TO THE KNOWLEDGE OF TWENTY-ONE SPECIES OF THE GENUS UPOGEBIA LEACH.
By J. G. de Man. *Martin Nijhoff*
9 guilders *The Hague*
$9\frac{7}{8} \times 12\frac{7}{8}$; 58 + 6 plates (paper)

A detailed systematic account, with abundant illustrations, of the taxonomy of the genus *Upogebia*, decapod crustacea belonging to the *Thalassinidae*, or *Callianassidae*.

SOCIAL LIFE IN THE ANIMAL WORLD.
By Fr. Alverdes.
Harcourt, Brace and Co., Inc.
$3.75 $5\frac{1}{2} \times 8\frac{1}{2}$; ix + 216 *New York*

An attempt at a comprehensive survey of animal sociology, the original German edition of which has already been noticed in THE QUARTERLY REVIEW OF BIOLOGY. The translation is excellent.

SCIENCE OF ANIMAL LIFE. *An Introduction to Zoölogy. Treating of Animals: Their Structure, Development, Reactions to Their Environment, and Relation to Man.*
By William M. Barrows. *World Book Co.*
$1.76 *Yonkers-on-Hudson, N. Y.*
$5\frac{1}{8} \times 7\frac{3}{8}$; ix + 389

A comprehensive high school text book of zoology, well illustrated, and excellently organized for teaching purposes.

A HANDBOOK OF THE BIRDS OF EASTERN CHINA (*Chihli, Shantung, Kiangsu, Anhwei, Kiangsi, Chekiang, Fohkien, and Kwangtung Provinces*). Part IV (*Containing Families Ploceidæ, Fringillidæ, Bombycillidæ, and Hirundinidæ*).

By J. D. D. La Touche. Taylor and Francis
7s. 6d. *London*

$6\frac{1}{4}$ x 9; 106 + 5 plates (paper)

Taxonomic, with notes on seasonal and geographic distribution, and, to a smaller extent, on habits.

BOTANY

UNTERSUCHUNGEN ÜBER DIE LICHTVERTEILUNG IN AVENA-KOLEOPTILEN UND ANDEREN PHOTOTROPISCH REIZBAREN PFLANZENORGANEN BEI EINSEITIGER BELEUCHTUNG.

Botanische Abhandlungen, Heft 12.
By Erich Nuernbergk. Gustav Fischer
19 marks *Jena*

$6\frac{1}{2}$ x $9\frac{1}{2}$; 162 + 12 plates (paper)

A contribution to plant physiology of the first importance. The author has devised a method of measuring with physical precision the penetration of light into plant tissue. The principle of the method is that the cross-section (or longitudinal section) of an organ illuminated from a certain direction is photographed at right angles to this direction, and the photograph so obtained is subsequently photometrically registered and measured. Experiments were conducted with five forms that have been much used in studies of phototropism, namely the hypocotyls of *Helianthus* and of *Panicum maliaceum*, the hypocotyl and coleoptile of *Setaria italica*, the coleoptile of *Avena*, and the root tip of *Sinapis alba*. Space is not available to summarize all the interesting results. But the type of result obtained may be indicated by the fact that in the case of *Helianthus*, with concentrated illumination with white light on one side, the intensity of illumination is 4.6 times greater on the lighted than on the shaded side. There is selective absorption for different regions of the spectrum, being $\frac{2}{3}$ for blue light if that for red light be taken as 1.

PLANT HUNTING

By Ernest H. Wilson. The Stratford Co.
$15.00 $6\frac{1}{4}$ x $9\frac{1}{2}$ *Boston*

Vol. I, xxix + 248 (paper)
Vol. II, ix + 276 (paper)

The author of these beautifully printed and superbly illustrated volumes is keeper of the Arnold Arboretum of Harvard University. He starts by saying that between 1899 and 1922 he "wandered about the world in search of plants." What an altogether delightful occupation!

> In these volumes I have attempted to give some account of the lands visited, of their discovery, their vegetation, and to tell in a general way also of the work done by early plant hunters. All parts of the world have added to the common store of garden material, but the countries sketched are among the richest sources of supply. Such a task as here attempted must, of course, be discursive since finality is obviously impossible. I have merely lifted a corner of the curtain so as to allow a peep at the general scene.

The result is a charming book, full of extraordinary interest, not only to the botanist but also to the general reader. The illustrations, of which there are 128 are a great feature of the work. They are mostly photographs of trees and the landscapes in which they occur. But they are superb photographs, of rare and beautiful trees. No gentleman's library should lack this book.

LES ÉQUISÉTINÉES DU QUÉBEC.
By Frère Marie-Victorin.
University of Montreal
$1.00 *Montreal*
6 x 9; xi + 137 (paper)

LES GYMNOSPERMES DU QUÉBEC.
By Frère Marie-Victorin.
University of Montreal
$1.00 *Montreal*
6 x 9; xii + 147 (paper)

SUR UN BOTRYCHIUM NOUVEAU DE LA FLORE AMÉRICAINE ET SES RAPPORTS AVEC LE B. LUNARIA ET LE B. SIMPLEX.
By Frère Marie-Victorin.
University of Montreal
50 cents *Montreal*
6 x 9; 22 + 3 plates (paper)

These papers constitute Nos. 9–11 of the contributions from the Botanical Laboratory of the University of Montreal. The first two are systematic floristic monographs, well arranged and carefully done, with good illustrations, dealing respectively with the horse-tails and the gymnosperms of Quebec. The third is a biometric study of three species of *Botrychium*, undertaken for the purpose of taxonomically distinguishing them.

PLANTS OF THE PAST. *A Popular Account of Fossil Plants.*
By Frank H. Knowlton.
Princeton University Press
$3.50 *Princeton, N. J.*
6 x 9; xix + 275

The author's purpose was to produce "a work of moderate size, written in non-technical language, that should set forth the salient facts regarding the plants that have clothed the earth from the time when life first appeared down to the present." This purpose has been excellently realized. The style is simple and straight-forward; the book is beautifully printed and illustrated; and the arrangement of the material is well calculated to sustain the interest of the general reader. We commend the book particularly to workers in other fields of science who wish to get a general idea of the present status of palaeobotany, without too much trouble.

COLORADO PLANT LIFE.
By Francis Ramaley. *University of Colorado*
$2.00 6 x 9; viii + 299 *Boulder*

This volume, in the series of Semi-Centennial Publications of the University of Colorado, is a highly successful attempt "to present in simple form some of the larger facts of plant life for the man or woman who is not trained in botany but who wishes to gain an appreciation of nature. Care has been taken to make all statements accurate, and it is hoped that the book will not seem shallow just because it is non-technical." Well illustrated, charmingly written, and sufficiently documented and indexed, the book can be highly recommended to the general reader and to the worker in other branches of science who wants to know something of the vegetation which clothes the earth about him.

ROOT DEVELOPMENT OF VEGETABLE CROPS.
By John E. Weaver and William E. Bruner.
McGraw-Hill Book Co.
$4.00 5¾ x 9; xiii + 351 *New York*

This is a companion volume to Weaver's *Root Development of Field Crops*, already noticed in these columns, and is largely based upon the authors' own investigations. Thirty-three separate chapters

are devoted to descriptions, mostly with original illustrations, of the root system of as many different garden vegetables. There is a bibliography of 182 titles, and an index. The book is an important contribution to the literature of ecology, as well as to that of horticulture and agriculture.

LA VIE DE LA CELLULE VÉGÉTALE.
By Raoul Combes. *Armand Colin*
9 francs 4¼ x 6⅝; 216 (paper) *Paris*

This excellent little treatise, which puts its emphasis mainly upon the functional aspects of plant cytology, discusses in detail the following subjects: The morphological constitution, origin and physiological rôle of the protoplasm of the plant cell; the chemical constitution of protoplasm; the form, origin, physiological function, and chemical constitution of the nucleus; general characters of plastids and mitochondria; the amyloplasts, chloroplasts, chromoplasts, oleoplasts, and proteoplasts. There is a bibliography covering nine pages.

PLANT RESPIRATION.
By S. Kostychev. Translated and Edited by Charles J. Lyon.
P. Blakiston's Son and Co.
$2.50 6 x 9; xi + 163 *Philadelphia*

Professor Lyon has done a real service to American students of plant physiology by providing this translation of Kostychev's treatise on respiration. It gives, as the translator says, a balanced, authoritative discussion of a subject which has made great advances in the twentieth century. The book is abundantly documented with citations of literature and will serve as a valuable reference work.

A LABORATORY MANUAL FOR THE STUDY OF GENERAL BOTANY.
By William E. Lawrence. *State College Press*
$1.80 6 x 9; 220 (paper) *Corvallis*

The third edition of a laboratory manual for a course in elementary botany, by the Associate Professor of Plant Ecology at the Oregon State College, based upon the idea that the "laboratory should be a place for study and investigation rather than merely an art or copy class. It should be a place where independent observations may be made and not a mere routine to be done for a grade."

THE ELEMENTS OF VEGETABLE HISTOLOGY.
By C. W. Ballard.
John Wiley and Sons, Inc.
$3.25 5½ x 8; xviii + 289 *New York*

The second edition, revised and enlarged, of a standard text, primarily intended for beginning students of pharmacy. The section on chemical reactions of plant tissues in particular has been enlarged. There is a brief bibliography of textbooks for reference use, and a detailed index.

THE STRUCTURE AND DEVELOPMENT OF THE FUNGI.
By H. C. I. Gwynne-Vaughan and B. Barnes.
The Macmillan Co.
$4.25 5½ x 8½; xvi + 384 *New York*

A systematic review, extensively illustrated, of the biology of fungi, with the principal emphasis on morphology but without neglecting the physiological side. There is an excellent section on mycological technique and a bibliography covering 28 pages of fine print. The book is a valuable contribution to botanical literature.

AN ELEMENTARY LABORATORY GUIDE IN GENERAL BACTERIOLOGY.
By Harold J. Conn.

The Williams & Wilkins Co.
\$4.00 6 x 9; ix + 165 *Baltimore*

A combined laboratory guide and notebook for elementary classes in general bacteriology, designed to accompany the Conns' textbook *Bacteriology*.

DICTIONARY OF BACTERIOLOGICAL EQUIVALENTS. *French-English. German-English. Italian-English. Spanish-English.*
By William Partridge.

The Williams & Wilkins Co.
\$4.00 $4\frac{7}{8}$ x $7\frac{1}{4}$; xi + 141 *Baltimore*

A brief but adequate dictionary of the equivalent English terms for French, German, Italian, and Spanish technical words used in writings about bacteriology.

DAS MIKROSKOP *und seine Benutzung bei pflanzenanatomischen Untersuchungen. Erste Einführung in die mikroskopische Technik, zugleich eine Erläuterung zu den Pflanzenanatomischen Tafeln von Niemann und Sternstein.*
By G. Niemann.

Creutz'sche Verlagsbuchhandlung
2.20 marks *Magdeburg*
$5\frac{1}{2}$ x $8\frac{3}{8}$; 104 (paper)

The third edition of a laboratory manual for the elementary study of the microscopic anatomy of plants.

MORPHOLOGY

CONTRIBUTIONS TO EMBRYOLOGY. *Vol. XIX, Nos. 98 to 108 (Publication No. 380). No. 98. The Menstrual Cycle of the Monkey, Macacus rhesus: Observations on Normal Animals, the Effects of Removal of the Ovaries and the Effects of Injections of Ovaries and Placental Extracts into the Spayed Animals, by Edgar Allen. No. 99. Embryology of the Neuromuscular Spindle, by Fidel Cuajunco. No. 100. Development of the Mesoblast and Notochord in Pig Embryos, by George L. Streeter. No. 101. Growth of the Human Foot and its Evolutionary Significance, by William L. Straus, Jr. No. 102. Lymphatics of the Fallopian Tube of the Sow, by Dorothy H. Andersen. No. 103. Correlated Physiological and Morphological Studies on the Development of Electrically Responsive Areas in the Cerebral Cortex of the Opossum, by Orthello R. Langworthy. No. 104. Histological Development of Cerebral Motor Areas in Young Kittens Correlated with their Physiological Reaction to Electrical Stimulation, by Orthello R. Langworthy. No. 105. On the Placentation of the Tridactyl Sloth, Bradypus griseus, with a Description of some Characters of the Fetus, by George B. Wislocki. No. 106. A Study of the Implantation of the Ovum of the Pig from the Stage of the Bilaminar Blastocyst to the Completion of the Fetal Membranes, by Chester H. Heuser. No. 107. Development of the Human Heart From its First Appearance to the Stage Found in Embryos of 20 Paired Somites, by Carl L. Davis. No. 108. Observations on the Ovary of the Opossum, Didelphis virginiana, by Carl G. Hartman.*

Carnegie Institution of Washington
\$6.25 paper binding *Washington, D.C.*
\$7.25 cloth binding
$9\frac{1}{4}$ x $11\frac{1}{2}$; 300

The papers in this superbly printed and illustrated volume are of such extraordinarily even and high quality that it is difficult to pick out any one for special mention without seeming to be unfair to the others, and lack of space makes it impossible to review them all. Several of them break new ground, and some of them, notably Davis's paper on the

development of the human heart, are certainly destined to become classics of anatomical reference.

GOETHE'S MORPHOLOGISCHE ARBEITEN *und die Neuere Forschung.*

By Valentin Haecker. *Gustav Fischer*
5 marks $6\frac{1}{2}$ x $9\frac{1}{2}$; vi + 98 (paper) *Jena*

An expansion of lecture material, which gives a better conception of the significance of Goethe's biological ideas in relation to the modern viewpoint than anything which has hitherto appeared. The topics discussed are: History of Goethe's botanical studies; The intermaxillary. First emergence of the idea of type; The vertebral theory of the skull; The osteological type; Goethe as physiologist; "Urpflanze" and metamorphosis of plants; Goethe's ideas regarding the developmental mechanics of plants; The spiral tendency of plants; Goethe as predecessor of Darwin. Altogether this brochure is a useful contribution to the history of science.

RECENT ADVANCES IN ANATOMY.

By H. Woollard. *P. Blakiston's Son and Co.*
$3.50 *Philadelphia*
$5\frac{1}{4}$ x 8; vii + 302

This little book maintains well the high standard of the "Recent Advances" series, other numbers of which have been noticed in these columns. The topics treated, in a readable and interesting fashion, are: Microdissection; tissue culture; oestrus, ovulation and menstruation; the youngest human ovum—the Miller ovum; growth centers and organisers; the morphogenesis of nerve fibres; vital staining; the origin of the cells of the blood; the cerebrospinal fluid; postural organs; the red nucleus; the extra-pyramidal system; the cerebellum; the projection of the retina in the central nervous system; protopathic and epicritic sensation; X-ray anatomy.

ÜBER DIE BESTIMMUNG DES ALTERS VON ORGANVERÄNDERUNGEN BEI MENSCH UND TIER AUF GRUND HISTOLOGISCHER MERKMALE. *Mit besonderer Berücksichtigung der Hämosiderinbildung bei Pferd, Rind und Hund.*

By Curt Krause. *Gustav Fischer*
6 marks $6\frac{1}{2}$ x $9\frac{1}{2}$; 120 (paper) *Jena*

A detailed account of an investigation of the time changes in pathological lesions, particularly those of an inflammatory character. The experiments were made on horses, cattle and dogs. There are extensive bibliographies following each section of the work.

EXTREMITÄTENENTWICKLUNG UND POLYDACTYLIE BEIM PFERDE. *Die Ontogenese des Hand- und Fussskelets, Varianten am Carpus und die Beurteilung der "entwicklungsbedingten" Polydactylie bei Equus caballus. Zoologische Bausteine. Band 1, Heft 3.*

By Fritz Drahn. *Gebrüder Borntraeger*
16 marks *Berlin*
$6\frac{1}{2}$ x 10; viii + 206 (paper)

A comprehensive morphological study, based upon a rich material, of polydactyly in the horse, prefaced by a detailed study of the normal ontogeny of the skeleton of the fore and hind feet. There is a bibliography of 77 titles, but no index.

PHYSIOLOGY

NOXIOUS GASES *and the Principles of Respiration Influencing Their Action. By Yandell Henderson and Howard W. Haggard. The Chemical Catalog Co., Inc.*
$4.50 6 x 9; 220 *New York*

Professor Yandell Henderson is the leading American investigator of the physiological effects of poisonous gases. He and his colleague, Dr. Haggard, have performed a useful service in concisely summarizing in this volume the present state of knowledge in this field. They classify noxious gases and vapors into three main groups, viz., asphyxiants, irritant gases, and volatile drugs and drug-like substances. Following a general introductory chapter, three chapters are devoted to a clear and concise account of the physiology of respiration. After a detailed treatment of the various noxious gases and vapors, the book ends with a chapter on prevention and treatment of poisoning by such substances. Each chapter is followed by a brief, but well chosen, list of references to the literature. The book is well indexed.

MUSCULAR MOVEMENT IN MAN: THE FACTORS GOVERNING SPEED AND RECOVERY FROM FATIGUE. *By A. V. Hill. McGraw-Hill Book Co.*
$2.50 6 x 9; 104 *New York*

This book records the results of the experiments on the physiology of athletes which the author made while holding the George F. Baker lectureship in chemistry at Cornell University last year. The general point of view is that of an engineering analysis of the work done by the human body, and an attempt at a rational explanation of how this work is done in terms of the physics and chemistry of the living substance. Professor Hill's work may truly be said to mark the initial development of a new era in human physiology.

LE SYSTÈME VEINEUX NORMAL ET PATHOLOGIQUE. *Guide des Malades et des Prédisposés. Varices—Phlébites—Hémorroides—etc. By Drs. Hugel and G. Delater. Gaston Doin et Cie*
15 francs $4\frac{1}{2}$ x 7; 182 (paper) *Paris*

This is supposed to be a guide for those who have or expect to have diseases of the venous system. The project is in many ways a curious one, and it is questionable whether there are many patients who would benefit by being handed such a book—even if it were written so simply that they could understand it all. Unfortunately, the authors seem to have kept in mind a medical audience as well as a lay one, and as a result they will probably "weary the unlearned, who need not know so much, and trouble the learned, who know it already." One wonders just what relation, if any, the writers bear to those who are selling the waters of Bagnoles. The section on therapeutics contains many exhortations to drink more of this particular fluid.

ÜBUNGEN AUS DER VERGLEICHENDEN PHYSIOLOGIE. *Atmung. Verdauung. Blut. Stoffwechsel. Kreislauf. Nervenmuskelsystem. By Hermann J. Jordan and G. Chr. Hirsch. Julius Springer*
19.50 marks *Berlin*
$6\frac{3}{8}$ x $9\frac{1}{2}$; viii + 272 (paper)

A very thorough and well worked out set of laboratory directions for a course in comparative physiology including both

vertebrates and invertebrates, covering the topics of respiration, digestion and metabolism, the blood and its circulation, and the nerve-muscle system. The directions for practical work are accompanied by explanatory text material. The whole presents the material for an extremely well-rounded course. American teachers of biology will do well to look into this book.

DER MESKALINRAUSCH. *Seine Geschichte und Erscheinungsweise.*
By Kurt Beringer. *Julius Springer*
18 marks *Berlin*
$6\frac{3}{4}$ x 10; v + 315 (paper)

This interesting volume reviews what is known about mescal, including its botany, chemistry and pharmacology, and then describes in detail an extensive experimental investigation of its physiological effects made by the author. More than a half of the book is devoted to detailed accounts of their introspective experiences by the persons who acted as subjects in the experiments. The book is a valuable contribution to the literature of physiology and psychiatry.

TIERPHYSIOLOGIE. *I. Stoffwechsel und Bewegung.*
By Konrad Herter. *Walter de Gruyter und Co.*
1.50 marks 4 x 6; 131 *Berlin*

A little handbook in the *Sammlung Göschen* on metabolism and movement, forming the first part of a treatise on animal physiology in this well-known series. It is intended primarily for high school teachers. The material is well chosen and presented in an interesting manner.

THE MENINGIOMAS *Arising from the Olfactory Groove and Their Removal by the Aid of Electro-Surgery.*
By Harvey Cushing. *Jackson, Wylie and Co.*
2s. 6d. $6\frac{1}{8}$ x $9\frac{3}{4}$; 53 (paper) *Glasgow*

This is the Macewen Memorial Lecture delivered at the University of Edinburgh in 1927. The solid surgical meat is prefaced by eight pages of delightful historical gossip, with some good stories, about Macewen, the Hunters, and other medical worthies.

ANIMAL NUTRITION.
By T. B. Wood.
University Tutorial Press, Ltd.
3s. 6d. $4\frac{3}{4}$ x $7\frac{1}{4}$; viii + 226 *London*

The second edition of a standard agricultural text by the distinguished professor of agriculture in the University of Cambridge. A few revisions of details constitute the only alterations from the first edition.

BIOCHEMISTRY

THE ANTISTERILITY VITAMINE FAT SOLUBLE E.
By Herbert McLean Evans and George O. Burr.
University of California Press
$5.00 10 x 13; 176 (paper) *Berkeley*

A monograph regarding the fifth definitely established vitamine. An account is here given of the work which the authors have done on the chemical purification of vitamine E. They conclude that: "There can be no doubt that there is a substance present in the active fractions which is specific for curing a specific type of sterility induced by certain purified diets. The cure has repeatedly been effected by as little as five milligrams

of the concentrated fractions fed on the day of positive mating. Controls have never given litters."

The topics discussed in this volume are:

General characterization of the sterility disease produced in rats by pure foods or other dietaries lacking fat soluble vitamine E; the histopathology of gestation in animals deprived of E; male sterility with dietaries lacking E; on the widespread occurrence of initial fertility in animals reared on simplified diets; distribution of vitamine E in foods of animal origin; distribution of the vitamine in foods of plant origin; proof of the existence of vitamine E in the tissues of animals reared upon natural foods and of its depletion in the tissues of animals reared upon synthetic rations; the survival of fertility in animals shifted from a diet possessing vitamine E to one deprived of it; the presence of vitamine E in the tissues of normal newborn young; proof of the use of vitamine E in the ordinary metabolic processes of the body; can an excess of vitamine E increase fertility beyond normal limits; the successful parental administration of vitamine E as a cure of sterility in female rats; the efficacy of a single curative dose of vitamine E administered at the beginning of gestation; determination of the minimal effective dose of vitamine E in the cure of sterility in the female rat; how late in gestation may we administer the vitamine to ensure the birth of living young; the solubility of the vitamine; stability of the vitamine; steps in the isolation and concentration of vitamine E.

This monograph is a worthy presentation of a fine piece of research.

LECTURES ON THE BIOLOGIC ASPECTS OF COLLOID AND PHYSIOLOGIC CHEMISTRY.

W. B. Saunders Company
$2.50 $5\frac{3}{8} \times 7\frac{3}{4}$; 244 *Philadelphia*

There are six of these Mayo Foundation lectures, by the following persons, and on the indicated topics: Principles underlying colloid chemistry, by Robert A. Millikan; colloid chemistry in biology and medicine, by Martin H. Fischer; the physical properties of protoplasm, by Robert Chambers; adsorption and vital phenomena, by Ross A. Gortner; the physics of the ultramicroscope and optical properties of colloid particles, by E. Franklin Burton; the biological effects of light, by William T. Bovie.

This volume constitutes a useful popular introduction to the colloid field.

KURZES LEHRBUCH DER CHEMISCHEN PHYSIOLOGIE.

By Ernst Schmitz. *S. Karger*
16.80 marks *Berlin*
$6\frac{1}{2} \times 9\frac{1}{2}$; vii + 384

The second edition of a general reading text of physiological chemistry for medical students. There is abundant citation of the literature up to the middle of 1926. The chief relative value of the book, in comparison with others on the subject, is in its judicious and skillful condensation of the essentials in a broad and actively progressing field of biology.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 244. Aminieren und Amidieren.*

By Hans Sickel. *Urban und Schwarzenberg*
10 marks 7 x 10; 200 (paper) *Berlin*

Lieferung 248. Elektrodialyse, by Mona Spiegel-Adolf; *Die Methoden zur Bestimmung der Beweglichkeit und der Ladung kolloider Teilchen*, by Arne Tiselius; *Molekulargewichtsbestimmung der Eiweisskörper durch Zentrifugierung*, by Theodor Svedberg.

Urban und Schwarzenberg
7 marks 7 x 10; 125 (paper) *Berlin*

Lieferung 254. Chemische Reaktionen Organischer Körper im Ultravioletten Licht und im Licht der Sonne.

By Franz Bachér. *Urban und Schwarzenberg*
32 marks 7 x 10; 630 (paper) *Berlin*

These three numbers of the Abderhalden Handbook deal with various aspects of

biochemistry. The first is highly technical, and only of interest to the chemist. The second is of particular interest to the student of colloids. The third, while dealing with chemical technique, will be indispensable as a reference work for everyone studying the effect of light on organisms with any attempt at thoroughness.

SEX

WOMAN AND LOVE.
By Bernhard A. Bauer. *Boni and Liveright*
$10 $4\frac{3}{4}$ x $8\frac{1}{4}$; Vol. I, 353; *New York*
Vol. II, xxvii + 396

This is another one of those books whose sale is "strictly limited to members of the medical profession, psychoanalysts, scholars, and to such adults who may have a definite position in the field of psychology or social research." The line of those failing to qualify under this "restriction" will form at the left, if any. The "chosen problem" of the book is "the loving woman." In the 776 pages of these two volumes about everything is said upon this entertaining subject that well could be. Unfortunately for the scholarly use of the book it is not documented, though mainly consisting of a wide-ranging review of certain parts of the literature of anthropology, ethnology, sociology, and psychology, nor does it contain an index. There is, to be sure, a "Bibliography" which does not quite fill one page, and in which the references are not cited with exactness or completeness. For those who love to read about the sexual act in all its relations this book can be recommended.

BIOMETRY

FREQUENCY CURVES AND CORRELATION.
By W. Palin Elderton.
Charles and Edwin Layton
15 shillings *London*
$5\frac{1}{2}$ x $8\frac{3}{4}$; vii + 239

This is a new and considerably enlarged and revised edition of the best textbook which has yet appeared for the student who wishes to learn the theory of Pearson's system of frequency curves. The chapters on correlation, contingency, probable errors, and goodness of fit have been rewritten and enlarged, and a new chapter on practical correlation has been added. An abridged course of reading is suggested to help those who are less interested in the mathematical side of the work and in the details of curve-fitting, but wish to know about the practical treatment of correlation, sampling, etc.

INTRODUCTION TO THE MATHEMATICS OF STATISTICS.
By Robert W. Burgess. *Houghton Mifflin Co.*
$2.50 $5\frac{3}{8}$ x $7\frac{3}{4}$; ix + 304 *Boston*

This volume accomplishes well the task implied in its title. It is intended to be of general usefulness to elementary students of statistics of all fields, and draws its examples from many of them.

PSYCHOLOGY AND BEHAVIOR

PHILOSOPHY.
By Bertrand Russell.
W. W. Norton and Co., Inc.
$3.00 $5\frac{1}{2}$ x $8\frac{3}{8}$; vi + 307 *New York*

The considerable popular interest in philosophy which is a curious phenome-

non of these present times will be enhanced by this volume. Bertrand Russell is not only an outstanding philosopher in his own right, but he can write more cleverly and melodiously than any other present practitioner in the field of the higher mysteries. This book is first of all a searching critique of theories of knowledge, with special attention devoted to the implications in this direction of behaviorism. With much of the behavioristic position Russell agrees, but finally breaks with it fundamentally, on a metaphysical point. Having cleared the ground of older theories the author ends with an exposition of the healing virtues of his own eye water. It is a good book; worth buying and studying.

ZUR PSYCHOLOGIE DER TIERE UND MENSCHEN.

By W. Betz. *Johann Ambrosius Barth*
7.50 marks *Leipzig*

$6 \times 9\frac{1}{4}$; xi + 206 (paper)

A wide-ranging discussion of all sorts of human affairs and interests, in the light of comparative psychology. The author writes with vigor and dash, and the book in consequence makes interesting reading. We like his contribution to the eugenics problem, in which it is suggested that if only the most superior men were not, as a rule, so weak and uncertain sexually they could easily have some hundreds of children apiece, any stupid moral restrictions being really easily removable, and then there would be some hope of occasionally getting an individual as much above Gauss, Faraday, or Kant, for example, as they are above the ordinary university professor, while the average would be raised up to the level of these great men.

THE SIXTH SENSE. *A Physical Explanation of Clairvoyance, Telepathy, Hypnotism, Dreams and Other Phenomena Usually Considered Occult. Forty Years of Study, Observation and Experiment.*

By Joseph Sinel. *T. Werner Laurie, Ltd.*
6 shillings net *London*

$4\frac{3}{4} \times 7\frac{1}{4}$; 180

This is an entertaining little book. The sense organ for "telepathic" and "clairvoyant" seeing is, according to Mr. Sinel, the pineal body. Children are more clairvoyant than adults because their pineal is bigger, and because the anterior fontanelle is not so tightly closed. Telepathy is the response of one brain to molecular vibrations in another. The simultaneous movements of a flock of starlings, for example, are taken as evidence of the occurrence of this phenomenon in animals. While it is very weak in spots, we think that most biologists will enjoy reading this volume. There is no law which compels anyone to agree with Mr. Sinel's theory.

THE MIND OF A GORILLA: PART II. MENTAL DEVELOPMENT. *Genetic Psychology Monographs, Vol. II, No. 6.*

By Robert M. Yerkes. *Clark University*
$2.00 *Worcester, Mass.*

6×9; 174 (paper)

This second report on the behavior of Congo, the young female gorilla brought from Africa by Mr. Ben Burbridge, maintains the high level of quality and interest set in the first report reviewed in an earlier number of The Quarterly Review of Biology. In the year which intervened between the two studies Congo unquestionably developed mentally. Of particular interest in this volume is the account of the beginnings of her sex behavior.

LE DESSIN ENFANTIN.
By G. -H. Luquet. *Félix Alcan*
20 francs $4\frac{3}{4} \times 7\frac{1}{2}$; 260 (paper) *Paris*

An interesting and scholarly discussion, with many illustrations, of children's drawings. The first half of the book deals with the psychological elements of children's drawings, and the last half with their evolution through successive stages. At the end a chapter is devoted to psychological and pedagogical conclusions.

THE MIND IN SLEEP.
By R. F. Fortune.
Kegan Paul, Trench, Trubner and Co., Ltd.
5s. $4\frac{3}{4} \times 7\frac{1}{4}$; xii + 114 *London*

This little book derives its chief interest from the examples of dreams which it describes in detail. All of them are of the type of mental conflict dreams, and in the cases given the side that wins in the dream is the side that in working life is not in the ascendant. The theoretical discussion is highly technical and chiefly of interest to the psychiatrist.

DAS RECHNEN DER NATURVÖLKER.
By Ewald Fettweis. *B. G. Teubner*
5 marks $6 \times 8\frac{3}{4}$; iv + 96 (paper) *Berlin*

An interesting digest of the anthropological literature regarding mathematical procedures among primitive peoples. The author finds a psychological phylogenetic parallelism to the ontogenetic development of the child in the highly cultured races, in respect to the evolution of mathematical thinking and technique. There is an extensive bibliography.

L'ESPRIT DE CONTRADICTION. *Ses Manifestations Individuelles et Collectives.*
By Paul Chavigny. *Marcel Rivière*
8 francs $4\frac{3}{4} \times 7\frac{3}{8}$; 160 (paper) *Paris*

A psychological and sociological study of the cantankerous person, who is "agin" pretty much everything, individually and collectively. It is an entertaining and, in some degree, significant book. There is a short bibliography appended.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

RACIAL OLD-AGE. *Being Further Adventures in Philosophy and Containing an Exoneration of Woman.*
By Henry Allen *Henry Allen*
$1.00 6 x 9; 34 (paper) *Seattle*

This is an amusing book. The Foreword reads as follows:

> The manuscript for this booket was rejected by two New York publishing firms. No doubt their judgment was correct, especially so as to the prospects of future sales. However, being of a perverse nature, I have decided to publish it with my own labour, using for that purpose a multigraph machine. This is my second experience of this sort. My first, a booklet on gravitational theory, has a perfect "No sale" record. I am much consoled, however, for on visiting an important public library I found neither my own book, nor works of Sir Isaac Newton nor any of the notable writings of Captain T. J. J. See.

The central thesis is put this way:

> Applying philosophical principles to the problem, the author was enabled to develop the factors for determining racial old-age to the point where it may be possible easily to recognize its presence in the human races and individuals. The broad principle involved is: The race or specie, as it grows old, repeats the indications of senility to be found in the individual of the race or specie as he or she grows old. As a corollary: The causes of racial old-age are the same as those that bring about stoppage of

further advancement and hasten premature old-age and death in the individual of the race or specie. In other words the underlying thesis of this booklet is an antithesis to the principle that in the embryological development and even in infancy the individual repeats, to some extent, the evolutionary history of the race.

The development of this theme leads to many entertaining ideas. The temptation to quote is great but we have space for only one sample: "And who is to blame for this increasing feminization of modern western societies, following the course of ancient societies in that respect? . . . . Man is to blame. He is almost wholly to blame. The proof is very simple. Even in these degenerate days our average modern she-man possesses a greater degree of sensitiveness than the average modern he-woman."

JINGO.
By John Veiby. *John Veiby*
$1.00 *South Bend, Ind.*
5 x $7\frac{1}{4}$; 157 (paper)

The object of this book is "to create interest in a national religion." And it is *some* religion! The women's headquarters are to be called *Jingo Inns*, each with a wise old woman to whom the young girls tell their troubles and are advised as to how to get out of them. A feast of sorrow may be instituted, which would resemble that of the ancient women weeping for the lost Adonis. The headquarters for the men are to be called *Jingo Taverns*. They will be like the old-fashioned saloons—"pleasant places of rest and recreation." The Jingo Sabbath is to be on Saturday and is to be started by taking a bath, then putting on special garments, and going to bed. "What happens after this, we do not know, and should not know." But sleep will be one of the things. "There must be guardians around the precincts of Jingo during the observance of the Sabbath, whose duty it would be to keep away disturbers of the peace, and also to wake up or call to order those within, if they should be visited by evil dreams or a nightmare, in short, see to it that the observance goes on peacefully, free and happy."

We recommend Jingo to our readers. There are few ways known to us to get more fun for a dollar.

LE RETOUR ÉTERNEL ET LA PHILOSOPHIE DE LA PHYSIQUE.
By Abel Rey. *Ernest Flammarion*
12 francs $4\frac{3}{4}$ x $7\frac{1}{2}$; 320 (paper) *Paris*

This volume, which appears in the *Bibliothèque de Philosophie scientifique*, is a detailed and scholarly discussion of the philosophical significance of modern thermodynamics and the kinetic theory of gases. The final position reached is that of Spinoza: "*Sentimus et experimur nos aeternos esse.*"

MEDICAL PALMISTRY *or The Hand in Health and Disease.*
By Katharine St. Hill. *Rider and Company*
7s. 6d. 6 x 9; ix + 132 *London*

This is the second volume of "The Book of the Hand." It is great stuff, considered as one more document to add to that large collection of treatises which evidence the odd ways in which the mind of *Homo sapiens* sometimes works. The authoress at the start enters a general disclaimer in this form: "apart from the hand I know but little of my subject." Every medical man who reads the book will agree. At the same time such a statement, which is reiterated on many pages of the book, does testify to real intellectual honesty. And

there is this further to be said that, after all, the lines of the hand are *a priori* no more inherently unpromising, considered as anatomical stigmata of constitutional anomalies, than are some of the characters seriously discussed in standard medical treatises on this subject.

EINSTELLUNG ZUR RÖNTGENOLOGIE. *Eine Untersuchung über die Einfügung der Röntgenstrahlenanwendung in Praxis, Forschung und Unterricht.*
By G. Holzknecht. *Julius Springer*
8.60 marks *Wien*
6 x 9; xii + 115 (paper)

One of the outstanding figures in roentgenology, a man who has watched the development of the speciality from its beginnings in 1895 to its enormous usefulness in 1926, feels the need for taking stock. The growth of the subject has been so rapid that there is much chaos and much need for finding out what is true and useful and what is not. He regrets that articles on the theory and practice of roentgenology are scattered through many books and journals where one would hardly expect to find them. They are written often from the points of view of many specialists who only incidentally are roentgenologists. The spread of interest in the subject is revealed also in the field of teaching, where it is hard to know what to do with students; should they get most of their knowledge of the roentgen ray in one department or should they pick it up here and there in the departments of physics, medicine, gastro-enterology, surgery, gynecology, urology, dermatology and orthopedics?

Similarly, what should be the training of the specializing roentgenologist? Should he ever be a layman? These and many other problems of great interest to American physicians are ably discussed. Unfortunately, Holzknecht's German may prove hard going for some.

CONTRIBUTION MÉTAPHYSIQUE *à la Méthode Expérimentale.*
By Louis Devos. *Georges Frère*
12.50 francs *Tourcoing*
6 x 9½; 56 (paper)

This booklet is written with such an enormous frugality of words that, frankly, we have not been able quite to grasp the point—at least not firmly. One thing, however, seems clear; that at the present stage of the development of the author's theory it concerns the physicist more than it does the biologist.

LA CONNAISSANCE SCIENTIFIQUE.
By Général Vouillemin. *Albin Michel*
9 francs 4⅜ x 7; 159 *Paris*

A philosophical and metaphysical discussion having for its purpose to show the limitations of the scientific method.

Vol. III, No. 3 September, 1928

THE QUARTERLY REVIEW
of BIOLOGY

THE GENE

By RICHARD GOLDSCHMIDT
Kaiser Wilhelm Institut für Biologie, Berlin-Dahlem

WITHOUT running the risk of exaggerating the geneticists may claim to have finally settled the following facts about the gene: 1. its real existence as a rather stable unit; 2. its position within the chromosomes of the cell; 3. the orderly arrangement of the genes within each chromosome; 4. the transmission of the genes through the generations of cells and individuals, generally without change of the nature of the gene; 5. the connection of definite genes as cause with every conceivable type of morphological and physiological character in the organism as effect. Thus the conception of the gene has become as firm a basis for the study of heredity as the conception of the atom for the study of physics. The next problems which have to be solved concern the nature of the gene and its action in producing the hereditary characters. The study of these problems has only begun. There is at present no way visible for a direct attack upon the gene which could reveal its nature. Only indirect ways are available, which might lead to more or less definite conclusions. Already quite a number of facts have been accumulated, which might serve as a starting point for further investigation. The following review will examine such facts and try to correlate them. The present writer has consistently worked in this direction and developed definite conclusions from experimental evidence, which so far as he can see are still the only ones covering the whole body of problems. He may therefore be excused if his own interpretations are placed in the foreground. However, the facts which will be recorded are facts, and everybody is welcome to give them another interpretation, provided it covers the same ground and is a better one.

A number of different ways are visible for the attack on our problem. In our opinion by far the best ought to be the study of the effects of the same gene in different quantities. If a gene has a different effect when present in different quantities and if these effects can be shown to follow any law a very considerable step will have been made towards the understanding of the action of the gene. This way of analysis was first opened by

the present writer; we may, therefore, begin with an evaluation of his primary facts and conclusions, which will be followed by a critical review of the different types of further evidence on the same point. These sections (A, B) will be followed by a review of the other methods of attack upon our problem and their results as we see them (C-F). Two short general sections (G, H) will conclude the paper.

A. THE EFFECTS OF THE SAME GENE IN DIFFERENT QUANTITIES

I. The genes of sexual differentiation

In a series of papers from 1911 to 1927 the present writer analyzed the case of experimental intersexuality in the gipsy-moth, which furnished him the first notions about the action of a gene. Neither the experiments nor the conclusions will be reviewed here in detail (A rather complete review up to 1926 is found in Goldschmidt, '27); only that part will be mentioned which is decisive for the present problem: viz. the proofs for our claim that in these experiments really different quantities of a gene were studied and further that these different quantities were linked up with typical effects.

One of the fundamental results of this work was the experimental proof that in dioecious animals both sexes contain the determiners or genes for the production of either sex and that the actual sex is determined by a quantitative relation or balance between these two sets of genes. As one of them (M in the Abraxas type, F in the Drosophila type) was shown to be situated in the X-chromosome and therefore present in one or two quantities, the other (F in the Abraxas type and M in the Drosophila type) being outside of the X-chromosome and always present in the same quantity, it became clear that the mechanism of the sex-chromosomes furnishes a method of associating the same dose of the one sexual determiner with either one or two doses of the other. As the two doses of the determiner within the sex chromosomes produce the sex of their own type (male—*Abraxas*, female—*Drosophila*), but with one dose present sex follows the determiners outside of the sex-chromosomes, the sexual decision is brought about by the relative quantities of the two types of genes according to the formula $F \gtrless {M \atop MM}$ (*Abraxas*) and $M \gtrless {F \atop FF}$ (*Drosophila*). This conclusion, which was inevitable from the writer's experiments, has since been corroborated by all the new evidence. Here then was the possibility of studying the effects of one gene in different quantities, other things remaining equal. We speak here of one gene F or M. Leaving aside certain autosomal modifiers which we found (and which were later similarly found by Bridges in *Drosophila*), we cannot prove experimentally that F and M are single genes. But all our large experimental evidence shows that they are inherited like single genes. For our conclusions it is then irrelevant whether the symbols F and M are the equivalents of single genes or of an unknown group of inseparable genes. If it is proven that the formulae in question are the true representation of the case—and this is proven—it follows that the quantity of each of these genes plays an important rôle in the action of the gene: a quantitative relation or balance has no meaning except in connection with the absolute quantities back of the proportion.

The full proof for these conclusions was derived from the experiments, in which forms were crossed which are distin-

guished by different but typical quantities of the F and M genes. The results are different combinations in which the normal balance as expressed in the above given formulae is disturbed because the quantity of M or F which has been introduced into the cross no longer balances the quantity of the other set (F or M). The result is male or female intersexuality of a definite degree up to sex-reversal in both directions, everything occurring in a most orderly way and completely in the hands of the experimenter. The decisive point is then, whether in these experiments a real proof has been furnished that the results are produced by the presence of different and typical quantities of the F and M genes.

There is indeed a very large amount of experimental evidence which consistently leads to the same conclusion. We may mention the fact that such diversified but typical results of a given cross as will be enumerated presently are completely explained and expected members of a series, namely: only males; only females; males normal and females of a definite degree of intersexuality; females and males *vice versa;* half the females normal, half intersexual; half or another ratio of males intersexual; 3 males: 1 female; 3 females: 1 male; the same 2: 1; only females and a few intersexual males etc. Further, if a given race is crossed in one direction with another test-race we can predict every result of crosses with all other races in every direction. Only this type of circumstantial evidence may be mentioned. But there are also direct proofs of the following types. First: The relative quantities of F and M for different races were determined from experiments on female intersexuality and the races arranged according to the values found. From the very different experiments on male intersexuality a similar determination was made; the two were always found to coincide. Further: Individuals of male gametic constitution (F) MM may be built up in which F comes from a race with high quantities of this gene and both M's from a race with a very small quantity of M. The result is a female in spite of male gametic constitution. We may then build up individuals in which F and one M remain as before but the other M is furnished by a third race of known behavior. The result, namely the production of male intersexes of a definite degree or normal males according to the race which furnishes the M, puts out of question any other explanation; it can only be understood, if really definite and typical quantities of F and M are involved. As a matter of fact any other interpretation of our experiments has never been proposed. Moreover it has become still more certain since triploid intersexes have been produced (Standfuss, '14; Bridges, '22; Goldschmidt and Pariser, '23; Meisenheimer, '24; Seiler, '27) where the different gene quantities are visibly given in the chromosome sets. (Full discussion in Goldschmidt, '27.) Thus it is claimed as a fact that in our work on intersexuality different quantities of one gene have been studied.

Now for the effect of these different quantities of genes. It has been demonstrated that intersexuality results if development of the individual proceeds up to a certain point, the turning point, with one sex and is finished after the turning point with the other sex, a demonstration which already has been produced for the intersexes of *Bonellia* by Baltzer ('14). The degree of intersexuality up to complete sex-reversal is determined by the earlier or later position of this turning point. This is not a hypothesis but a fact proved by morphological and embryological study (see

Goldschmidt, '17, '20c, '22, '23c, '27b). Thus we have the four sets of facts: 1. At the beginning of development two sets of genes, male and female, are present in definite quantities; 2. The relation or grade of balance of these two quantities decides whether normal sex is developed or a definite step in a continuous series of intersexuality up to sex-reversal; 3. Normal sex, increasing intersexuality and sex-reversal are determined by the non-occurrence or earlier and earlier incidence of the turning point; 4. The time of incidence of the turning point is a simple function of the relative quantities of the *M* and *F* genes, namely of the degree of their unbalance. These facts, based on an extraordinarily diversified but always consistent set of experimental and morphological data, are linked together by the conclusion that *a*) both the *F* and *M* genes produce chains of reactions of definite velocities, *b*) that these velocities are *ceteris paribus* proportional to the absolute quantities of the genes, *c*) that the series of turning points are points of intersection of the curves of the two reactions, and *d*) that therefore the position in time of these points of intersection is a simple function of the proportion of the two quantities of the genes in question. It should be emphasized that every criticism of these conclusions is worthless without a proof that either the underlying facts are not correct or that other and better conclusions can be drawn from the facts.

Here then has been derived for one type of genes, the sex-genes, a definite idea of their action: the production of chains of reaction of definite velocities which are a function of the quantity of the gene in question. As early as 1917 the present writer, after having studied another case, which led to the same conclusions, had enlarged them to apply to all genes. In '20b and '27a he used this insight as the basis for developing a general theory of heredity, a theory which has been called by some critics the beginning of a new era in genetics and by others bunkum, neither sound genetics nor sound physiology; a reception which in view of historical parallels seems rather encouraging to the author. But this generalized theory may be dismissed here and only such material reviewed as furnishes further evidence on the nature and action of the gene.

2. *Multiple allelomorphism*

The different sex genes of the races of the gipsy moth behave genetically like multiple allelomorphs; our work therefore demonstrated for the first time that a series of multiple allelomorphs of a definite gene was really a series of different quantities of this gene. There is a possibility that sex-genes are different from other genes; discarding this the present writer came to the conclusion ('17, '20b, '24) that most if not all multiple allelomorphs are of the same order. Two ways of proving this generalization were visible, first the indirect way of demonstrating that as in the case of intersexuality series of multiple allelomorphs were linked up with reactions of definite velocities, and second the direct way of proving the quantitative nature of multiple allelomorphs. The first line of demonstration was followed by the present writer in his work on the markings of gipsy-moth caterpillars ('17, '20b, '24), after Sewall Wright had come very near to the same result in his work on rodents ('16, '25). A similar demonstration for non-multiple allelomorphic genes was given recently by Ford and Huxley ('27). The second direct way of approach has only recently been made possible through the brilliant work of Sturtevant on the bar series of *Drosophila* ('25).

Wright studied a multiple allelomorphic series of a diluting gene for coat and eye color, which may be combined with different factorial constitutions of other genes and produces in these combinations closely parallel series of effects. This leads him to the conclusion (Wright in Castle and Wright, 1916, p. 71) that "it seems most satisfactory to attempt to explain the results on the basis of four quantitative gradations of one factor, which determines the amount of the basic color-producing enzyme." In a recent publication ('25) the same author returns to this subject and concludes "that the factors of the albino series determine the rate of some one process fundamental to all pigmentation . . . . . " The experiments of the present writer, which have led to the actual demonstration of such curves of velocity in a parallel case, have been overlooked by this author, which makes his work still more important as a verification of our conclusions.

This work of the present writer ('17, '20b, '24) has enabled him to study the effects of a multiple-allelomorphic series of a gene on a character in different stages of development. The characters in question are the markings of the caterpillars in different geographic races of the gipsy-moth, characters which can be traced through the different stages of development of the caterpillars. From the manifold facts which the study of the races and their crosses has brought to light only those pertaining to the present question may be mentioned. The two extreme races are that with light-marked caterpillars, retaining their pattern throughout life up to the last instar, and a darkly pigmented race not exhibiting the pattern of light markings. Between these stand other races which in young stages show the light pattern, which however is covered in the course of development with dark pigment so that grown up caterpillars of such races cannot be distinguished from those of the dark pigmented races. We might call this the intermediate type. Between this and the dark races as well as the light ones many other races are found showing the same type of developmental change from light to dark but in different degrees. Light and dark are a simple pair of allelomorphs and all the other intermediate types are based on multiple allelomorphs of these genes. This is not surprising as we know that in the silk worm also many types of markings form such allelomorphic series. If now a light race is crossed with a dark one the F_1 caterpillars are light in young stages and become dark in later stages of development, thus behaving exactly like the pure intermediate races. If we plot curves of the changes of pigmentation during development in the different pure races, dividing the scale from light markings to no markings into classes we get empirical curves of the progress with time of pigment deposition in the skin of the larvae. If this more or less increasing deposition of pigment is the result of a chain of reactions, these curves demonstrate the typical velocities of the reaction. (For details see the full presentation in '24). If these empirical curves are plotted for the pure races as well as their hybrids we realize at once that the different multiple allelomorphs of the pigmentation factor have the effect of producing pigmentation curves of different and specific velocities, the velocities of hybrids lying between those of the respective pure races. Here then we have first the exact demonstration that such different states of a gene, which are called multiple allelomorphs, produce reactions of different and typical velocities; further a very strong intimation that these multiple allelomorphic genes are different quantities of the same gene, as

otherwise it could hardly be understood that hybrids between light and dark races have the same curve as pure intermediate races (The effect of the allelomorphs $AiAi$ = effect of $Ad + Al$).

The work of Ford and Huxley ('27) does not deal with multiple allelomorphs but with ordinary genes controlling eye-color in *Gammarus*. But as eye colors in other animals (*Drosophila*) furnish typical examples of multiple allelomorphism it might be quoted at this point. The authors found in *Gammarus chevreuxi* races with different rates of velocity in regard to the darkening of eye-pigment, as shown in empirical curves. It was shown that the hereditary difference of the two races was that of a simple Mendelian gene, thus demonstrating that certain genes are causing definite rates of reaction. In this case there was no way visible to connect the different rates of the specific developmental process with different gene quantities. On bringing together facts of this type with such ones as reviewed before the present author has been led to consider whether or not the majority of mutations consist in changes of the typical quantity of the gene ('17, '20b, '23a, '27a).

As mentioned before a direct demonstration that multiple allelomorphs are in fact different quantities of the same gene can be found in Sturtevant's ('26) work on the bar eye of *Drosophila*. It is known that bar is a dominant mutation from normal, reducing the number of facets. A further reduction was found by Zeleny in his mutation ultrabar, which behaved genetically as a multiple allelomorph to bar and normal. Sturtevant however proved in a series of exceedingly beautiful experiments that ultrabar is the product of unequal crossing-over resulting in the location of two bar genes in one chromosome. Thus he was able to build up individuals with 1, 2, 3 and 4 such bar genes and to study the effects on facet number. He further found another mutation in the bar series, infrabar, having an intermediate effect between normal and bar. But this gene has some special features in regard to the phenotypical effect as well as in its behavior in temperature experiments. Therefore Sturtevant does not consider it as a member of the otherwise quantitative series. The present writer is of different opinion, but for the present purposes a discussion of this point might as well be left out of consideration. Here then we have a series of genotypes behaving experimentally like multiple allelomorphs. But it is an experimental fact that the majority of the members of the series are formed by different quantities of a gene. This series is linked with a series of facet numbers exactly parallel to these quantities. An analysis of the following tables computed from Sturtevant's data will illustrate our point. If B is the gene for normal, B_1 for infrabar, B_2 for bar the combinations shown in table 1, page 313, have been produced.

We can arrange this table so that the different possible types of heterozygous forms parallel the respective homozygous forms and get the table (the numbering of the combinations is the same as in the first table), shown in table 2, page 313.

This table seems to the present writer very impressive. With the single exception of No. 13 all the heterozygous combinations closely parallel the homozygous series in regard to decreasing numbers of facets. Sturtevant has now proved conclusively that No. 4 has four quantities of the gene B_1, No. 5 two quantities of B_1 and B_2 each, No. 6 four quantities of B_2, etc. This series 1 to 6 affects increasingly the number of facets in negative order. Among the members

TABLE 1

NUMBER	HOMOZYGOUS formula	phenotype	FACETS	NUMBER	HETEROZYGOUS formula	phenotype	FACETS
1	$\frac{B}{B}$	normal	779.4	7	$\frac{B}{B_1}$	normal-infrabar	716.4
2	$\frac{B_1}{B_1}$	infrabar	320.4	8	$\frac{B}{B_2}$	normal-bar	358.4
3	$\frac{B_2}{B_2}$	bar	68.1	9	$\frac{B}{B_1B_1}$	normal-doubleinfrabar	200.2
4	$\frac{B_1B_1}{B_1B_1}$	double infrabar	38.2	10	$\frac{B}{B_1B_2}$	normal-barinfrabar	50.5
5	$\frac{B_1B_2}{B_1B_2}$	barinfrabar	26.7	11	$\frac{B}{B_2B_2}$	normal-ultrabar	45.4
6	$\frac{B_2B_2}{B_2B_2}$	double ultrabar	24.1	12	$\frac{B_1}{B_2}$	infrabar-bar	73.5
				13	$\frac{B_1}{B_1B_1}$	infrabar-doubleinfrabar	138±
				14	$\frac{B_1}{B_1B_2}$	infrabar-barinfrabar	37.8
				15	$\frac{B_1}{B_2B_2}$	infrabar-ultrabar	41.8
				16	$\frac{B_2}{B_1B_1}$	bar-doubleinfrabar	38.3
				17	$\frac{B_2}{B_1B_2}$	bar-barinfrabar	37
				18	$\frac{B_2}{B_2B_2}$	bar-ultrabar	36.4
				19	$\frac{B_1B_1}{B_1B_2}$	doubleinfrabar-barinfrabar	27.9
				20	$\frac{B_1B_1}{B_2B_2}$	doubleinfrabar-ultrabar	26.7
				21	$\frac{B_1B_2}{B_2B_2}$	barinfrabar-ultrabar	24.1

TABLE 2

HOMOZYGOUS Number	Facets	HETEROZYGOUS WITH B Number	Facets	HETEROZYGOUS WITH B_1 Number	Facets	HETEROZYGOUS WITH B_2 Number	Facets
1	779.4	7	716.4	7	716.4	8	358.4
2	320.4	8	358.4	12	73.5	12	73.5
3	68.1	9	200.2	13	138±	16	38.3
4	38.2	10	50.5	14	37.8	17	37
5	20.7	11	45.4	15	41.8	18	36.4
6	24.1						

HETEROZYGOUS WITH B_1B_1 Number	Facets	HETEROZYGOUS WITH B_1B_2 Number	Facets	HETEROZYGOUS WITH B_2B_2 Number	Facets
9	200.2	10	50.5	11	45.4
13	138±	14	37.8	15	41.8
16	38.3	17	37	18	36.4
19	27.9	19	27.9	20	26.7
20	26.7	21	24.1	21	24.1

of this series No. 4 is certainly a quantitative condition of B_1, No. 6 of B_2, and No. 5 of B_1 and B_2. Therefore the difference between B_1 and B_2 ought to be quantitative. If this is the case all the possible combinations of 2, 3, 4 quantities of B_1 and B_2 must form parallel series to the homozygous series, which is the case. Finally the gene B with all its combinations falls exactly in line in these different series and therefore must also be regarded as belonging to the series of quantities. In other words, there is a number of different equations involving B, B_1, B_2, which can be solved only if B, B_1, B_2 have typical but different numerical values.

Thus we regard this case as conclusive proof of the quantitative nature of multiple allelomorphs. Our second result was that these different quantities of a gene are linked with reactions proceeding at different rates proportional to the respective quantities which produce the typically different phenotypical result. The present writer has analyzed this case in the same direction and found that the results can best be represented this way. (For details see Goldschmidt, '27a, p. 63 ff. It ought to be mentioned that on p. 68, 69, of the work in question a *lapsus calami* occurred. The tables on these pages have erroneously been calculated as differences instead of as proportions. If corrected the similarity between result and calculation is still better.)

In concluding this section a general point may be mentioned shortly. Many years ago Baur in discussing our views in regard to the quantity of the gene remarked that it is impossible to imagine that the genes are always present in the same quantity. Lillie ('27) has recently taken up the same argument. Speaking of possibilities I might venture the opinion that if chromosomes were invisible bodies and their numerical constancy only deduced from genetic experiments, the same argument would immediately be at hand. The same applies to every numerical constancy in organisms, the segments of insects and the number of cells in the nervous system of *Ascaris*. I cannot see why it is more difficult to conceive a typical number of molecules for a given gene. But finally these considerations are superfluous because it is an actual fact that the effect of a gene is different and typical if present in 1, 2, 3, 4 quantities, which would be hard to account for if the unit quantity was not of fixed magnitude.

B. THE EFFECTS OF THE SAME GENE IN DIFFERENT QUANTITIES IF MORE THAN ONE GENE IS INVOLVED

Genes in different quantities may also be studied in cases of either absence or multiplication of parts of chromosomes, of whole chromosomes, or of whole chromosome sets. In such cases, however, the conclusions are subject to uncontrollable error. The result attributed to different quantities of one gene may be decisively influenced by the corresponding difference in many or all the other genes. If whole chromosomes or even whole chromosome sets are involved the additional effect of the change of the nucleo-plasmic ratio may come into play. Thus experiments of this type can only furnish additional evidence, which has to be handled cautiously, weighing the different possibilities for each case.

The smallest deviation from the single gene evidence is obtained if only a small number of genes are involved, as in the deficiency studies of the Drosophila workers. After Bridges has shown that the effects of the deficiency are of the same order as in the haplo IV, one can safely assume that deficiencies are real absences or at least complete inactivations

of the genes involved. Thus in such cases a gene may be studied in a single quantity in comparison with the double quantity in homozygous condition and the plus or minus-double quantity in normal heterozygous condition. The source of error consists in the presence of a few other genes in the same condition. Bridges noticed first and other writers, notably Mohr, obtained the same result, that characters produced by a single gene, the partner being totally absent, appear exaggerated: characters produced by only one gene *a* differ still more from the normal type than the same characters produced by *aa*. Bridges' explanation of this phenomenon by genic balance is well known. If according to our views the decisive point is the quantity of the gene, an explanation of this phenomenon should be found when multiple allelomorphs are involved in the same experiment. If multiple allelomorphs are different quantities of the same gene complete absence of one gene is to be regarded as the end point of the series. Mohr ('27) was able to study such a series, the well-known white series of eye colors in *Drosophila*, in the case of deficiency. If white, the lowest member of the series, is combined in heterozygous condition with the other members, it has a diluting effect on the phenotype. If the members of the series are combined with deficiency (viz. Wo, W_1o, W_2o instead of Ww, W_1w, W_2w,) the effect is still further dilution. Total absence of *w* therefore acts like a further still lower member of the series. The present writer feels unable to draw any other conclusions from such facts than that we see here the effects of a different quantity of the gene. In a paper read at the International Genetics Congress, 1927, Mohr produced new facts, which he thinks are in favor of our conclusions.

It is obvious that under these circumstances the phenotypic effect called exaggeration has to be understood in the same way as the effects of other different multiple allelomorphs, namely through the medium of different velocities of reaction. How this can be done in detail has been discussed in the present writer's book ('27a, p. 78 ff.).

The next possibility of studying different quantities of a gene without involving all genes is in trisomic forms as notably given in Blakeslee's work on *Datura* and the triplo-IV form of *Drosophila* (Bridges). Here of course the causes of error are greater, because whole chromosomes are involved with the quantitative disturbance of all their genes and a possible general effect (nucleo-plasmic ratio) in addition. In the case of *Datura* more general results of the trisomic constitution have been studied than effects of the three quantities of individual genes. But in the triplo-IV Drosophilas the effects of three quantities of a gene could be studied. Judging from the case of deficiency and haplo-IV with exaggeration, the respective phenotype in the triplo-IV is expected to be exaggerated in the opposite direction than in the deficiency case, because three quantities of the gene might again be the same as a higher multiple allelomorph. In fact these are Bridges' results, which however are interpreted differently by him, namely by genic balance (see later). At this point a word ought to be inserted about a closely related phenomenon. According to the workers on *Drosophila* many dominant mutations in that form are lethal, when homozygous; homozygous deficiency is lethal; absence of both IV-chromosomes is lethal; on the other hand four IV-chromosomes are also lethal. There is probably a consensus of opinion, that in all these cases some balance in the cooperation of the genes, or expressed more correctly in the effect of the genes,

necessary for normal development is disturbed. It would be difficult to translate this general statement into definite terms without using the idea of definite gene-quantities linked with definite rates of reaction.

A further method of studying genes in different quantities is furnished by cases of polyploidy, especially triploidy and tetraploidy. Here the difficulties of clear conclusions are still greater because all genes are involved and the effect of one of them in three or four quantities will be completely outweighed and a normal balance restored, since the whole system is built up on the basis of such different quantities. There is the additional effect of the nuclear plasmic ratio, which in these cases is a well known fact (see Wettstein's review). Therefore conclusions regarding our problem can hardly be expected, with two exceptions, namely when sex is involved in the triploid intersexes where the presence of the X-chromosome mechanism makes it possible for sex genes to act in different quantities which are not corrected by parallel changes in the quantities of all the other genes; and further when in triploid hybrids the phenomenon of dominance is involved. That triploid intersexuality leads indeed to the same conclusions in regard to the sex-genes and their action as diploid intersexuality has been repeatedly shown by the present writer ('23, '25, '27). The case of dominance will be discussed later.

C. EVIDENCE DERIVED FROM THE STUDY OF THE EFFECTS OF EXTERNAL CONDITIONS UPON THE PHENOTYPICAL EFFECT OF A GENE

Thus far we have reviewed the evidence furnished by the study of genes in different quantities. Another method of attacking the problem is the study of the action of particular genes under different environments. The first definite information from experiments made with this end in view, was found in the present writer's experiments with intersexes. If the results of his analysis of the phenomenon of intersexuality are correct, namely that intersexuality is produced if the two simultaneous chains of reaction, those of female and male differentiation, have a point of intersection during development, it follows that intersexuality could be produced within normal genic constitution, if such a point of intersection could be induced experimentally. The only visible method for such an experiment was the use of low temperatures, on the supposition that the sex-differentiating reactions and the other reactions controlling rate of development might have a different temperature coefficient. Such experiments were performed many times, always with positive result. ('21). As a matter of fact Kosminsky ('09) had already performed the same experiment with the same result without knowledge of intersexuality and all the questions discussed here, and has since enlarged his former results ('24). One further consequence (which Prof. J. Huxley kindly suggested) is that similar experiments performed with intersexual stock must shift the degree of intersexuality towards higher intersexuality. This experiment was also performed successfully.

These experiments led to a very important conclusion: The effects of temperature (or other experimental conditions) may be phenotypically identical with the effect of a different gene, the reason being that in both cases the rate of a definite reaction is changed, in the same sense. This consideration furnished a simple explanation for ('20b) such phenomena as e.g. the phenotypic identity of heritable geographic forms with forms produced in temperature experiments on butterflies

in the classic researches of Dorfmeister, Standfuss, Merrifield, Weismann; or for the behavior of seasonal-dimorphic butterflies, as has been discussed in detail by the present writer ('17, '20b, '23c, '27a) and controlled experimentally by his former student Süffert ('24); or further for the many instances of phenotypic identity of modifications and mutations. For our present discussion, however, the important point is the demonstration that definite genes are really connected with definite rates of reaction.

There have since appeared other investigations which in our opinion lead to the same result. We mention first Zeleny's ('23) work on the influence of temperature upon the bar eye in *Drosophila*. This author concludes from his experiments: "Perhaps the most interesting point in connection with the present data is the demonstration that they furnish of the fact that the gene ultrabar has the same type of reaction as a temperature difference. It is possible to state the effectiveness of particular germinal factors in terms of the corresponding effects of temperature." And further: "In view of the fact that temperature is effective only during a few hours of larval life, it may be considered that the initial steps in the formation of ommatidia are confined to a definite embryological period. (This applies also to the butterfly wing. R. G.) The length of this period is determined by the general physiological processes of the larva, while the rate of formation of ommatidia during the period is a function of special processes, which have a different coefficient." The present writer thinks that with the introduction of the conception of velocities of reaction into Zeleny's results they fall completely into line with his conclusions. In addition we recall that it has been shown for the bar-genes with which Zeleny worked that it is their quantity which counts.

A very remarkable piece of work which leads in the same direction has been done by Plunkett ('26). He studied the effects of temperature upon bristles in *Drosophila*, trying to exclude all disturbing factors. The results—mainly a consistent reduction of bristle number with increasing temperature—were minutely analyzed. Some of his conclusions are: The essential difference between the dichaete and wild-type flies (so far as bristles are concerned) is the velocity of a bristle-reducing reaction. The effect of this continuous reaction, namely bristle or no bristle, takes place if the concentration of the produced substance equals or exceeds a certain threshold value. The action of the gene, then, is the production of a chain of reactions, namely: the gene produces from a protoplasmic component, the distribution of which means localization, a catalyst *R*, the concentration of which is typical for the respective gene. For this production of *R* the gene itself may be the catalyst. The concentration of *R* is again proportional to the velocity of a reaction, the already mentioned reaction for the production of bristles, conceived as decomposition of a thermolabile bristle-forming catalyst *B*. Here then we have again all the elements of the present writer's old conception of the action of the gene by definite velocities of reactions, producing the formative substances. But there is one difference: not the quantity of the gene but the quantity (concentration) of a product of the gene, the catalyst *R*, is linked with the different velocities. We have seen already that ample proof is existant to show that the quantity of the gene itself is decisive, whatever the intermediate points of the chain or reactions might be. Thus Plunkett's work, as far as it goes, confirms the present writer's former conclusions. It might be added that Plunkett draws general conclusions from his analysis

which are indeed a restatement of the present writer's ('17, '20b, etc.) views (unknown to the author), e.g. "It is a tenable hypothesis that this is the way in which all genes produce their observed effects: by differential acceleration of various reactions in the organism" or "In such a complex system of successive and 'competing' reactions the differential acceleration of certain ones can produce great, and apparently complete differences in the end results. It is not at all impossible that the metabolic and morphogenetic differences among species, individuals and tissues may be entirely due to differential acceleration, by specific catalysts, of the infinite variety of 'spontaneous' reactions possible to the components of protoplasm." Readers of our papers (notably '20b and '22a) will be familiar with these conclusions, even to the expression "competing reactions." One of the writer's papers ('23c) is entitled "Contributions to the theory of differentially accelerated reactions" (literally "tuned reaction-velocities"). It is further remarkable that proceeding in his analysis Plunkett comes to views regarding the relation of these genic reactions to morphological localizations, approaching very closely those which the present author developed in his book, which was through press when Plunkett's paper appeared. This encourages the present writer to believe that after all his theory of heredity is "sound genetics and sound physiology."

D. EVIDENCE DERIVED FROM THE STUDY OF DEVELOPMENT OF MENDELIAN CHARACTERS

In reviewing the case of multiple allelomorphs for the pigmentation of *Lymantria* we have already met with the study of Mendelian characters during development. A number of other facts are known, which furnish further insight into the mode of action of the gene. Two students of Haecker (who introduced for this type of study the term phenogenetics) Pernitzsch and Schnakenbek ('13) showed that the difference between normal and albinotic axolotls is mainly a result of different rates of growth and multiplication of the melanophores and xanthophores. The present writer ('20, '23c) found that the differently colored parts of the pattern of a butterfly wing are the product of different rates of differentiation of the scales, with the effect that the scales in different parts of the pattern are ready for the deposition of pigments at different times. This demonstrated the presence of a series of differently timed reactions working together in a definite way (see detailed discussion, '27a). In a paper on the color-types of the fish *Oryzias* Goodrich ('27) finds that the different Mendelian phenotypes are produced by deposition of different quantities of pigment in given numbers of cells. This might of course be expressed in terms of reaction velocities.

In this section such general studies on development might also be mentioned as do not relate to definite genes but rather to the general unanalyzed genotype. We think of the work of Stockard, Newman, Harrison, Spemann, Brandt. Here many instances are found demonstrating the importance of timed reaction-velocities in connection with the genotypic constitution. (For particulars and discussion see Goldschmidt, '27a.)

E. EVIDENCE DERIVED FROM HETEROZYGOSITY

There is, I believe, a consensus of opinion that dominance is not a property of an individual gene but one of the results of the interaction of the genes, including the one in question, in producing the

visible character during development. In trying to formulate an opinion about the production of this phenomenon two primary possibilities are given. The dominant and the recessive gene might act independently, the result being determined by some resultant of both actions. It is evident that in this case the phenomenon ought to be explained on the same basis as the phenomenon of epistasis. For this we have shown in a special case, namely the competing reactions produced by the sex-genes, that the result depends upon the two respective velocities of the competing reactions and a third variable, an independently determined point in development, determined by some or many other genes. In this case the dominant and recessive, or the two epistatic genes, might differ qualitatively or quantitatively. In any case the phenomenon of dominance or epistasis can be understood only on the basis of a set of differential reactions of definite velocities (for details see Goldschmidt, '27a). The second possibility is that in the heterozygote the dominant and the recessive gene do not act independently. If we assume the difference between these two genes to be one of quantity, this would mean that, e.g., the allelomorphs of the respective quantities 10 and 6 would have a single combined action based on the quantity 16. In our experiments on intersexuality we have produced experimental proofs (see '23b, '25a and much unpublished material) that actually this is the case if two different quantities of an allelomorph are combined (male intersexes built up from three races). If the same applies also to other cases dominance and its different degrees would result from a system of reactions where one, with its specific velocity, is the product of the combined action of the added quantities of the two allelomorphs, the others being determined by the other genes controlling the exactly timed reactions necessary for development. How such systems work is discussed in Goldschmidt, '27a, p. 67 ff. Here the argument is also applied to such cases as the dominance within the bar eye series of *Drosophila*. It seems therefore to the present writer that the phenomenon of dominance lends further support to the idea that genes are connected with timed chains of reactions proportional to their quantities. In harmony with this interpretation are the facts known about the results of the combination of two recessives with one dominant gene (Correns, Wettstein, Bridges, Morgan). In some cases two recessives dominate one dominant; in others the opposite is true. It seems difficult to explain such facts without assumptions of the foregoing type.

There might be mentioned also the phenomenon of change of dominance during individual life. The present writer ('17, '20b, '24) first analyzed such a case genetically in the already quoted work on the pigmentation of caterpillars. In F_1 between a light and a dark race young caterpillars are light and change later towards the dark side. The study of the pigmentation curves in such cases showed that the facts have to be explained on the basis of typical curves of reaction of definite velocities in the parents and intermediate velocity in the hybrid. The phenomenon then again supports the general idea. Honing ('27) and Ford and Huxley ('27) have since analyzed similar cases and accepted our explanation.

F. THE CASES OF VARIEGATION

In recent genetic literature the study of a certain type of variegation has aroused great interest and has been used as a starting point for conclusions upon the nature of the gene. Speaking generally these varie-

gations are produced on the basis of a single Mendelian unit. In appearance they show "a continuous series of quantitative variations ranging from apparently deep self colors with only occasional color changes that are apparent through a series of dilute self-colors with all gradations of color from deep red to whitish and with increasing numbers of dots, splashes, lines, bands and larger segments of darker and lighter colors; and through a series of variegations varying in pattern from very heavy to extremely light." This description by Eyster ('28) of the pericarp case in maize covers also the more or less similar types in other cases, viz. *Antirrhinum*, *Mirabilis*, *Capsella*, etc. These unstable types are not confined to different individuals but occur within the same individual. It has therefore to be explained why on the basis of an apparently single Mendelian gene a complex mosaic is produced with a number of typical features. The first idea is that there is something unusual the matter with the gene in question, Correns ('19) directly speaking of a sick gene. All explanations which have been tried, though looking at first sight very different, are of much the same order if viewed from some distance. All interpretations agree that something happens to the gene in question so that different cells are produced and the stage of development in which this something occurs determines the resulting pattern. The event in question is regarded by Emerson ('13, '17, '22) as a temporary inactivation of the gene. Baur ('24) also does not wish to touch the old conception of the gene as the genetic unit. But realizing that some diversity of the genic basis is needed to explain the facts he assumes that a number of unilocal genes are present which recombine in different ways. Correns ('19) was the first to make the revolutionary step of explaining the facts by assumptions regarding the finer structure of the gene. He writes:

> "In order to have at least a model one might assume that the gene consists of a large molecule to which the same sidechain of atoms is attached, say, ten times. This number might be mutable, might undergo changes in the plus or minus direction under unknown conditions 'external' for the gene. To each number of these sidechains would correspond a definite ratio of white and green in the mosaic plant . . . . . The difference in this interpretation . . . . . would be that the state of the gene, the number of sidechains, attached to the gene molecule, is not constant, but that new chains could be added or old ones detached, and this during ontogenesis of the individuals."

Here then we have already a somewhat quantitative conception based on the assumption of a complex structure of a gene which may change quantitatively in regard to definite parts of the whole. A step further leads to the theory of Anderson and Eyster ('24, '25, '28). The last named author assumes that the facts can only be explained if a quantitative segregation of parts of the gene takes place in development. The gene, then, is regarded as composed of a constant number of genomeres or gene elements, which may or may not be chemically identical. The genetic difference between pigmented and pigmentless forms is given in the genomeres, the genomere *C* being mutated into *c;* both genes contain the same number of genomeres, either *C* or *c*. If, however, only a certain number of genomeres mutate from *C* to *c* an unstable gene with two types of genomeres is produced, the gene of the variegated forms. This gene may be divided into its genomeres during somatic mitosis, giving different combinations of genomeres up to a complete separation of the two types *C* and *c*. It is clear that all the facts can be represented by this conception, which is very closely akin to that of Correns.

If we compare these different concep-

tions of Baur, Correns, and Eyster we see at once that all of them start from the necessity, derived from the experiments, of introducing some quantitative element into the conception of the gene in order to have a chance of sorting out such quantities. Baur prefers a definite quantity of different unilocal genes, Correns accepts a definite quantity of permutable side chains, and Eyster believes in permutable quantities of different genomeres. The reader of the present writer's work will at once realize how much these assumptions may be simplified and brought in line with all our other knowledge of the gene if the unilocal genes, sidechains and genomeres are replaced by molecules (or group of molecules) of the substance called a gene. If, as we believe we have proved, one of the essential properties of the gene is its quantity, the situation is the following: The "pigmented" gene has a definite quantity, say ten molecules. The mutation to pigmentless consists in changing this quantity into four molecules. Normal, stable genes have the elementary property of being "adsorbed" in the chromosome, always in their characteristic quantity, at least in all cells up to the point of their final determination. Unstable genes, properly called by Correns sick genes, lack something in their physico-chemical properties necessary for constancy in their number of molecules. In mitosis therefore the twenty molecules present at the time of fission of the chromosomes may be "adsorbed" by the two daughter chromosomes say as 12 and 8. It is not necessary to work this out in detail: The result must necessarily be the same as in the other hypotheses. The advantage is, besides the fitting into the general theory of the gene, that no different types of genes or genomeres with quantitive assortment are needed but simply the definite quantities of the one gene substance reckoned in numbers of molecules (or molecule-compounds). Thus the facts about unstable genes seem to add new material to the already broad basis of our general conclusions.

G. THE NATURE OF THE GENE

There are no direct facts giving information about the nature of the gene. If our conception is correct that the gene is a definite quantity of something (of course qualitatively different things in many different genes) linked with a chain of reactions with a velocity proportional *ceteris paribus* to its quantity, it does not single out a definite type of chemical substance. However all general considerations have led practically everybody who discussed the problem since Driesch in premendelian days and Hagedoorn in early Mendelian days to regard the gene as a type of enzyme and specifically as an autocatalyst. The present writer has also joined this view, the only alternative to which is at present agnosticism. Of course this gives no information about the members of the chain of reactions catalysed by the gene. If Plunkett (1926), for example, concludes from his experiments "that the gene acts as a true catalyst" which as the first step in the chain of reactions catalyses the production of another catalyst, which in its turn is connected with further reactions of definite rate, this is not a different view from ours, as Morgan ('26) seems to believe, but a specification of a more general assumption. Further discussion of this point does not seem profitable at present.

H. THE INTERACTION OF GENES IN DEVELOPMENT

If we try to formulate definite ideas regarding the gene and its mode of action we do it with the end in view of understanding the rôle of the genes in directing

typical development. It is therefore not surprising that the present writer tried to enlarge the conception of the gene and its action, which he regards as proven by experiment, into a general theory of heredity ('17, '20b, '27a). The general basis of this is the conception of differential and balanced (*abgestimmte*) reaction velocities. We have seen already that Plunkett's work led him to accept this conclusion. The present writer has further tried ('27a) to work out in detail this general conception and to apply it to the details of development as analysed in experimental embryology. Studying the facts in the light of the basic conception he arrived at a consistent and simple theory of heredity, which brings together the facts of genetics as well as of experimental and descriptive embryology. This theory, which certainly goes beyond the arbitrary limits set by some to "sound" genetics and to "sound" physiology, will not be reviewed here. But it might at least be compared briefly with the only other attack on the problem, Bridges' conception, not yet elaborated, of the genic balance. This will be of special interest because the type of facts (intersexuality) and the type of explanation (balance of sex-genes) from which Bridges and the present writer started was identical. Bridges' idea will best be presented in his own words ('22):

"Each gene is essentially a factory which is manufacturing a characteristic set of chemical products that are delivered to the common cytoplasm, and that produce development through interaction with each other and with materials from outside. But since the chemicals produced by the different genes are different, some genes will have much effect upon one character and little effect upon another, so that a relatively small proportion of the genes will be actively concerned in producing any given character. Some of these genes tend to make the character more pronounced and others tend to make it less pronounced, so that the grade of development actually realized by each particular character will be determined by the equilibrium between its modifying genes. The forms into which a given character can be modified are in general quite diverse, but for the sake of simplicity we may call them all + or − modifications. If the effectiveness of a given + or − modifier is changed by mutation, the grade of the character will shift correspondingly."

This statement is rather general and it will hardly be possible to account for orderly development without substituting some concrete conception for the generalities. When we read that "the grade of development actually realized by each particular character will be determined by the equilibrium between its modifying genes" we see at once, I believe, that this statement is endowed with a concrete meaning only if we make the step from the balanced genes to the balance of the action of the genes. Such a balance however, working in development, can hardly be conceived otherwise than in the form of balanced rates, of a harmony of timed chains of reactions, playing together in an orderly, balanced, properly tuned way. In other words, the conception of genic balance, if interpreted in concrete terms, leads to our theory of balanced action of the gene.

LIST OF LITERATURE

Baltzer, F. 1914. Die Bestimmung des Geschlechts nebst einer Analyse des Geschlechtsdimorphismus bei *Bonellia*. Mitt. Zool. Stat. Neapel, 1922.

1925. Untersuchungen über die Entwicklung und Geschlechtsbestimmung der *Bonellia*. Publ. Staz. zool. Napoli, 6.

Baur, E. 1924. Untersuchungen über das Wesen, die Entstehung und Vererbung von Rassenunterschieden bei *Antirrhinum majus*. Bibl. Genet., 4.

Bridges, C. B. 1917. Deficiency. Genetics, 2.

———. 1922. The origin of variations in sexual and sexlimited characters. Amer. Nat., 56.

BRIDGES, C. B. 1925. Sex in relation to chromosomes and genes. Amer. Nat., 59.

CORRENS, C. 1901. Bastarde zwischen Maisrassen. Bibl. Botan., 53.

———. 1919. Vererbungsversuche mit buntblättrigen Sippen I. Sitzungsber. Preuss. Ak. Wiss., 34.

EMERSON, R. A. 1917. Genetical studies of variegated pericarp in maize. Genetics, 2.

———. 1922. The origin of variations. Amer. Nat., 52.

EYSTER, W. H. 1924. A genetic analysis of variegation. Genetics, 9.

———. 1925. Mosaic pericarp in maize. Ibid., 10.

———. 1928. The mechanism of variegations. Verhdlg. Intern. Congr. Vererbg., Berlin, 1927.

FORD, E. B. and HUXLEY, J. S. 1927. Mendelian genes and rates of development in *Gammarus Chevreuxi*. Brit. J. Exp. Biol., 5.

GOLDSCHMIDT, R. 1911. Ueber die Vererbung der sekundären Geschlechtscharaktere. Münch. med. Wochenschr.

———. 1912. Erblichkeitsstudien an Schmetterlingen I. Zeitschr. f. indukt. Abstammungs- u. Vererbungslehre, 7.

———, and POPPELBAUM. 1914. Erblichkeitsstudien an Schmetterlingen II. Zeitschr. f. indukt. Abstammungs- u. Vererbungslehre, 11.

———. 1915. Vorläufige Mitteilung über weitere Versuche zur Vererbung und Bestimmung des Geschlechts. Biol. Zentralbl., 35.

———. 1916. Experimental intersexuality and the sex-problem. Amer. Nat., 50.

———. 1916a. A further contribution to the theory of sex. Journ. of Exper. Zool., 22.

———. 1917. A preliminary report on some genetic experiments concerning evolution. Amer. Nat., 52.

———. 1919. Intersexualität und Geschlechtsbestimmung. Biol. Zentralbl., 39.

———. 1920. Untersuchungen zur Entwicklungsphysiologie des Flügelmusters der Schmetterlinge. Wilh. Roux' Arch. f. Entwicklungsmech. d. Organismen, 47.

———. 1920a. Mechanismus und Physiologie der Geschlechtsbestimmung. Gebr. Borntraeger. Berlin.

1920b. Die quantitativen Grundlagen von Vererbung und Artbildung. Roux' Vorträge und Aufs., H. 24.

——. 1920c. Untersuchungen über Intersexualität Zeitschr. f. indukt. Abstammungs- u. Vererbungslehre, 23.

——. 1921. Zur Entwicklungsphysiologie der Intersexualität. Naturwissenschaften, 9.

GOLDSCHMIDT, R., and SAGUCHI. 1922. Die Umwandlung des Eierstocks in einen Hoden beim intersexuellen Schwammspinner. Zeitschr. f. Anat. u. Entwicklungsgesch., 65.

———. 1922a. Untersuchungen über Intersexualität II. Zeitschr. f. indukt. Abstammungs- u. Vererbungslehre, 29.

———, and PARISER, K. 1923. Triploide Intersexe bei Schmetterlingen. Biol. Zentrlbl., 43.

———. 1923a. Das Mutationsproblem. Zeitschr. f. indukt. Abstammungs- u. Vererbungslehre, 30.

———. 1923b. Untersuchungen über Intersexualität III. Ibid., 31.

———. 1923c. Einige Materialien zur Theorie der abgestimmten Reaktionsgeschwindigkeiten. Wilh. Roux' Arch. f. Entwicklungsmech. d. Organismen, 98.

———. 1924. Untersuchungen zur Genetik der geographischen Variation I. Ibid., 101.

———. 1925. Bemerkungen über triploide Intersexe. Biol. Zentralbl., 45.

———. 1925a. Ueber die Erzeugung der höheren Stufen männlicher Intersexualität bei *Lymantria dispar*. Ibid.

———. 1926. Nachweis der homogametischen Beschaffenheit von Geschlechtsumwandlungsweibchen. Ibib., 46.

———. 1926a. The quantitative theory of sex. Science, 64.

———. 1927. Die zygotischen sexuellen Zwischenstufen und die Theorie der Geschlechtsbestimmung. Ergebn. d. Biologie., 2.

———. 1927a. Physiologische Theorie der Vererbung. Berlin. J. Springer.

———. 1927b. Weitere morphologische Untersuchungen zum Intersexualitätsproblem. Ztschr. Morphol. Oekol., 8.

GOODRICH, H. B. 1927. A study of the development of Mendelian characters in *Oryzias latipes*. J. Exp. Zool., 49.

HAECKER, V. 1918. Entwicklungsgeschichtliche Eigenschaftsanalyse. (Phänogenetik.) Jena.

HONING, J. A. 1927. Erblichkeitsuntersuchungen an Tabak. Genetica, 9.

KOSMINSKY, P. 1909. Einwirkung äusserer Einflüsse auf Schmetterlinge. Zool. Jahrb. (Syst.), 27.

———. 1924. Ueber Erzeugung von Intersexen bei *Stilpnotia salicis* L. Biol. Centrbl., 44.

LILLIE, F. R. 1927. The gene and the ontogenetic process. Science, 66.

MEISENHEIMER, J. 1924. Die Vererbung von Art und Geschlechtsmerkmalen bei Biston-Artkreuzungen. Zool. Jahrb. Abtg. Allg. Zool., 41.

MOHR, O. L. 1927. Exaggeration and inhibition phenomena. Avh. Norske Vidensk. Ak. Oslo, 1, No. 6.

MORGAN, T. H. 1926. Genetics and the physiology of development. Amer. Natur., 60.

——, BRIDGES, C. B., and STURTEVANT, A. H. 1925. The genetics of *Drosophila*. Bibliogr. Genet., 11.

PARISER, K. 1927. Die Zytologie und Morphologie der triploiden Intersexe des rückgekreuzten Bastards von *Saturnia pavonia* L und *Saturnia pyri*. Schiff. Ztschr. Zellf. mikr. An., 5.

PERNITZSCH, R. 1913. Zur Analyse der Rassenmerkmale der Axolotl. Arch. mikr. Anat., 82.

PLUNKETT, C. R. 1926. The interaction of genetic and environmental factors in development. J. Exp. Zool., 46.

SCHNAKENBECK, W. 1921. Zur Analyse der Rassenmerkmale der Axolotl II. Ztschr. indukt. Abstl., 27.

SEILER, J. 1927. Ergebnisse aus der Kreuzung parthenogenetischer und zweigeschlechtlicher Schmetterlinge. Biol. Centrbl., 47.

STANDFUSS, M. 1914. Mitteilungen zur Vererbungsfrage. Mitt. schweizer anatom. Ges., 12.

STURTEVANT, A. H. 1925. The effects of unequal crossing-over at the bar locus in *Drosophila*. Genetics, 10.

SÜFFERT, F. 1924. Bestimmungsfaktoren des Zeichnungsmusters beim Saisondimorphismus von *Araschnia levana-prorsa*. Biol. Centrbl., 44.

WETTSTEIN, F. VON. 1924. Morphologie und Physiologie des Formwechsels der Moose mit genetischer Grundlage I. Ztschr. indukt. Abstl., 33.

——. 1927. Die Erscheinung der Heteroploidie besonders im Pflanzenreich. Ergebn. d. Biol., 2.

WRIGHT, S. 1916. An intensive study of the inheritance of color, etc. Carn. Inst. Publ., 241.

——. 1925. The factors of the albino-series in guinea pigs. Genetics, 10.

ZELENY, C. 1923. The temperature coefficient of a heterozygote. Biol. Bull., 44.

SUB-HUMAN CULTURE BEGINNINGS

By A. L. KROEBER

University of California

As ONE of the social sciences, Anthropology deals with that relatively closed system of phenomena called culture. This system is closed in the sense that life is a closed system. The biologist does not repudiate the results of physics and chemistry; but his task is with phenomena and problems on the specific level of life. He expects that his findings will ultimately be convertible into findings in terms of the inorganic sciences, yet he realizes that his approach must be in terms of his own. Just so the social scientist does not assert that human social activities are controlled by a metaphysical something unrelated to organic forces. But he does believe that the first explanation of cultural phenomena must be in cultural terms. He sees every cultural phenomenon preceded by other phenomena and related to them; and this relation, on a cultural or social or supra-organic level, he feels must first be clarified and intellectually organized. Only then can the approach from the organic or physiologic level, and still later that from the chemical one, lead to fruitful results. Anything else leads to short-circuiting of understanding.

THE ORGANIC BASIS OF CULTURE

Within the social sciences, history, economics, politics deal with only part of the totality of culture manifestations. They are, therefore, essentially restricted to consideration of phenomena which lie wholly within the system of culture. These are purely social sciences. Anthropology has a somewhat different outlook. So far as it concerns itself with races, with human beings respectively set apart and united into groups by a common heredity, Anthropology is organic or natural science. So far as it examines institutions, customs, folk-ways, inventions, and speech, it is supra-organic or cultural. By common consent the study of the earliest and most backward peoples and cultures has been left to Anthropology. The significance of these incipient cultures is obviously not so much intrinsic as in the light which they may shed by enabling a wider and fuller range of comparisons on the nature of culture as a whole. The relation of the system of culture to the organic system is thereby thrust into the foreground. I have on another occasion defined the special sphere of Anthropology as being concerned with the interrelation of the organic and the cultural. I have also been criticised, perhaps justly, for abandoning the program after formulating it. The reasons were the obvious one of difficulty and the present slender promise of productive results. It is however now and then worthwhile to envisage the larger problems which in candor we must admit to be still largely insoluble, in order that our daily work as scientists may remain as much as possible in touch with the fundamentals of science, and not degenerate

into routine. This is my apology for venturing upon a subject in which as yet it seems impossible to be definite without remaining cautiously narrow, and in which on the other hand one can not be broad without becoming indefinite. This subject is: the organic basis and origin of culture.

There are three principal approaches to the question of the origin, or original nature, of culture. These are, first, the prehistoric or archaeological record; second, ontogenetic development in the infantile human individual; and third, comparison with those of the infra-human animals most likely to manifest anticipations of cultural activity.

The archaeological approach has the virtue of giving us, so far as it goes, an objective mass of evidence. It is further advantaged in that its phenomena occur associated in nature with geological and paleontological phenomena, so that they can be arranged with considerable certainty in an order of time which is objectively founded. The archaeological method, however, suffers from the fact that its data are primarily tangible, whereas much of culture, in one aspect its very essence, is intangible. Archaeology recovers some of the tools, materials, and mechanical processes of the past; but we can only conjecture the thoughts and institutions and human relations which accompanied these tools and processes.

The ontogenetic approach—child study—is full of promise. But scientific recording in it has been almost as scant as recognition of the promise held by further data has been wide-spread. We have hardly got beyond the stage of realizing that the first necessity is to rid ourselves of a mass of implicit but confusing interpretations that block progress. In this clearing of the ground the Behaviorist school of psychologists have done valuable work. Too often, however, they have acted as though this first step were also the final one. And whatever their own attitude, they have certainly helped create the impression that human beings come into the world with practically no equipment. This, if true, would make the acquisition of culture by each individual almost entirely a matter of life experience in contact with other individuals already possessing culture. Carried to its logical conclusion, such an interpretation would pull the organic basis out from under culture, while at the same time dealing with it not as a system in itself, but as a series of accidental events. The Behaviorists are evidently far more interested in method than in results; indeed pride themselves on the fact. What they cannot rigorously prove they will have nothing to do with; and too largely the outcome is an attitude as if what they prefer not to operate with did not exist.

The comparative approach through examination of infra-human behavior also has its limitations. It is again a difficult field, in which controlled facts are scarce, and misinterpretations easy, especially those of the anthropomorphizing kind. Domesticated animals must of course be used with caution. They have not acquired culture, but they have come under its influence. The most highly socialized organisms, sometimes presenting astounding analogies to the human societies which carry culture, occur among the insects, a group differing thoroughly in structure, and apparently in the nature of their reactions, from ourselves. The upshot of the work of the most critical students in the field, such as Wheeler, seems to be a stressing of the essential difference between insect and human societies, a pointing out that the similarities are analogies and not realities.

THE BEHAVIOR OF APES

Fortunately, however, the last fifteen years have seen a burst of interest in those of the mammals most nearly related to ourselves, the Primates, and among the Primates in the anthropoid or man-like apes. This interest has been partly popular, but has also been reflected in the endeavors of biologists and psychologists to secure reliable evidence and a sound understanding of the behavior of these apes. The work of Koehler, Kohts, Boutan, Yerkes, Furness, has been as critical as is possible in the present development of science. Controlled experiments have been added to systematic observations. Strangely enough, not one of the studies of the great apes has been made by an anthropologist. But there is in this at least the advantage that an anthropological interpretation cannot be challenged on the ground of bias or preconception.

All of the four types of man-like apes have been studied, but the chimpanzee has provoked most interest. The gibbon is very different from ourselves in proportions and behavior; he is thoroughly arboreal. The orang approaches him in this respect; he possesses a sluggish and melancholy temperament. The gorilla, perhaps anatomically closest to man, has been difficult to capture and keep in confinement. His study has yielded some results; but his attitude toward human beings is aloof. The chimpanzee is about equally similar to man, shows definite responsiveness to human association, and is relatively hardy and docile.

THE CHIMPANZEE

The chimpanzee's life is primarily terrestrial, although he is a splendid climber. The body is not carried fully erect, and the knuckles frequently touch the ground in walking; but locomotion is on two feet. The differentiation of the limbs into a locomotory and a manipulative pair is not as marked as in man, but approaches it. There are few if any human manual abilities which the chimpanzee does not possess. He is endowed with much greater strength. The available data suggest that his muscular power may be estimated at three times our own.

The infant chimpanzee begins to teethe within two months, walks at the end of six, has all its milk teeth within twelve months, and possesses at that age sufficient muscular coördination to secure for itself part of its food, although it may continue to nurse. A period of playfulness and activity follows. Growth is at first slower than in man, but rapid toward adolescence. Sexual maturity comes at about eight to ten years in females and ten to twelve in males. Accompanying sexual maturity there is a change of temperament. Playfulness diminishes, indolence and irritability increase, the individual becomes less exuberant in his manifestations of sociability, and, on account of his great strength, somewhat dangerous. This appears to be part of a wider process involving a slowing down or at least change in direction of what we call intelligence. In experiments, young chimpanzees have made the best performances. The one adult female of Koehler, for instance, was rated by him near the bottom of his list of seven immature chimpanzees. A human parallel is obvious. The duration of chimpanzee life is not known, but is estimated at not very much less than that of man.

CHIMPANZEE PSYCHOLOGY

The senses of the chimpanzee are similar to our own. Sight, which is the easiest to test in both species, is much alike in perception of color, form, and distance.

Hearing appears to be about as acute as in man. Taste and smell are utilized very much as by ourselves, primarily with reference to food. All in all, the sensory equipment is definitely analogous to that of man, and different from that of sub-primate mammals.

This is expectable. A body like ours with senses like those of a dog is a combination hardly to be anticipated in nature. The chimpanzee's use of his senses is also human. If he sees something out of his reach but with a string attached to it, he pulls the string with as little hesitation as a human being. If there are several strings, he draws the one lying in most direct line toward himself; or if only one is actually in visual contact with the desired object, he pulls that one. After all, he possesses a string-pulling mechanism—arms and hands and fingers; and this would serve him in little stead if he saw blurred instead of clearly, or if his ability to interpret spatially were deficient.

If food is put on the ground outside a barred window, a string attached to it and led indoors, and an ape allowed to survey the situation, he quickly hauls the food up on the cord. A dog fails to grasp the situation. He may starve before he takes the cord in his mouth and backs across the room to haul the food in. He does not see the relation of food, string, and himself; he cannot connect or synthesize them.

Tests in which an animal is put under conditions where it makes a selection between several possible acts but is compelled to defer action on the choice, have yielded in the rat a memory span of a few seconds; in the dog, a few minutes; in the ape, according to Kohts, a quarter of an hour, and, according to statements of Yerkes, under favorable conditions several hours. In the human being the range varies from a few minutes in a small child to years or the entire life in adults. But such deferred choices have something artificial about them. Rats do not encounter swinging doors and electric flash-lights in nature. The memory span of mammals may be indefinitely long for places, persons, and experiences. What the experiments seem essentially to show is that sub-human animals all make poor showings in tests, the dog slightly surpassing the rat, and the chimpanzee the dog. Laboratory tests are after all devised in culture primarily for organisms that have culture. We may simplify them and yet make them extremely difficult for an organism constructed differently from ourselves. They tend to be weighted humanly, whether we want it or not.

As regards imitativeness, observations are at variance. Koehler interprets the chimpanzee as much less imitative than does Yerkes. But the latter found a gorilla non-imitative almost to the point of being negatively suggestible. This, however, was with reference to use of appliances or solution of problems such as the animal would not encounter in nature. When it came to eating new foods, the gorilla was willing to follow example—provided no persuasion was applied and it could withdraw to make the test in seclusion. Emotional factors are evidently of the greatest influence as regards imitativeness; and these are conditioned by the social relations in which the ape finds itself. Yerkes' orang and chimpanzees were almost members of his household. Koehler's apes lived primarily in a colony of their own. It is clear that they learned very little from one another in the solution of posed problems. Imitativeness is evidently called out largely by association with human culture.

LACK OF SPEECH AMONG APES

On the side of speech it is agreed that the ape is completely deficient in imitativeness. Observations and experiments are uniformly negative. At this point the close human associations and manual adaptations of Yerkes' animals are of high significance. They did learn to brush their teeth, to spit, to eat with a spoon, to go to bed, and a hundred other things which the family was doing. They could not be taught to speak at all.

Furness, by long and repeated practice, taught his young orang to say "Papa," and apparently to realize that this sound complex in some way related to her master. Whether the animal recognized that "Papa" was Furness' name, as Furness believes, is another question. When he goes on to tell how the animal, as she was being carried into water which she dreaded, clung to him and cried "Papa! Papa! Papa!", the facts may be accepted, and yet the interpretation that the ejaculation was an "appeal" in the human sense is wholly subjective. Next, the same orang was taught to pronounce the word "cup." Her tongue was repeatedly pressed back with a spatula into position for articulation of the hard "c" or "k" sound. After she had learned to release the consonant and the vowel, the lip motion of the "p" was added and mastered. The poor brute managed after a time to produce a pretty fair rendition of the word "cup." But there is nothing to show that it meant anything to her. Pronunciation may have seemed nothing more than an end in itself; perhaps a game, or an intrinsically meritorious act that earned approval. Once at night, on awakening, she spontaneously uttered the word. Furness thought that she might be thirsty, offered her a drink, and the animal accepted. But, who knows why? Almost pathetic was the way in which the docile little animal was trying her best to coöperate without apparantly grasping the point. After a time she offered to push the spatula against her tongue with her own hands. Here was something that master wanted, and she was eager to help. But what it was all about, or that she might utilize the lesson, quite likely never entered her consciousness. Furness quite properly concludes that the apes do not possess the faculty of language in the proper sense of the word.

Parallel are the results of Boutan, who worked with a gibbon, a particularly vocal species. The gibbon, he finds, is capable of no more than pseudo-language. Its sounds are like those of the other mammals in expressing emotions; they do not convey anything objective. Utterances relieve the utterer: there is no semblance of their being purposive as regards conveying information. The chimpanzee, in fact, does not confine himself to vocal utterances: when frightened he rattles a tin pan or thumps the wall of his cage. It is clear that we are beyond the realm of what can profitably be construed as language when we are driven to include the rattling of pans.

All in all, the data at hand are unanimous to the effect that the speech faculty of the apes is substantially on a par with that of a normal six-months old human infant: namely, nil. When we inquire why this is, it seems likely that however we may paraphrase it in more technical terms, the old reason literally holds: animals do not talk because they have nothing to say.

This fact is particularly striking because the structure of the mouth parts of the apes is so similar to that of man that there is no doubt that they could render reasonably close approximations to the sounds of human speech. They might talk with

a brogue, but we could understand them. What a parrot does when with his horny beak he produces effective imitation of a soft lip sound like "p," a primate could obviously do at least as well, so far as his anatomical apparatus is concerned. Yet he never tries to speak, nor apparently can he be induced to try, no matter how close his associations with humans.

HAVE APES A CULTURE?

There are three historic definitions of man designed to set him off functionally from the other animals: man is the speaking animal; man is a political animal; and man is the tool-using animal. Other phrasings, such as the fire-using or clothes-wearing animal, are evidently included under the more general category of tool-using. We have considered the first of these criteria, that of speech, and found it to hold. The second definition goes back to Aristotle. It has been said that, the connotations of words having changed, Aristotle, if he were living now and speaking in English, would make his definition run that man is a social animal.

We still know very little as to the kind of society the apes maintain in a state of nature. Their behavior in captivity, with dependance primarily on human beings instead of fellow apes, evidently is little indication. With a few exceptions, those observed in captivity have been immature. Natural history observations will obviously be extremely difficult. That the apes are sociable is evident but not to the point. Dogs, birds, some other species, are highly sociable toward human beings. Of course if man were not endowed with a gregarious impulse he could not have developed culture; but something more than gregariousness is needed to produce culture; otherwise cattle would possess it. Now it is conceivable that the chimpanzee and gorilla possess something more than sociability or personal attachments; that they pass down from individual to individual and from family to family certain forms or patterns of relation to one another—traditional group habits, which may have begun to take on something of the color of institutions. But that this actually has happened without the presence of speech is difficult to conceive; and there are no positive indications whatever as to the existence of such incipient institutions. It would not be difficult to project backward from the simpler human social institutions to something that seems still simpler and expectable among apes. But experience has shown that such reconstructions are always in part misleading, and quite likely to be unfounded. As regards the question, then, whether the apes are in any rudimentary degree social animals in the sense that man is institutional, we can at present answer with nothing more than a question mark.

It may be thought that there are some evidences warranting a less skeptical attitude. Koehler reports that when a pair of his young chimpanzees in playing began to stamp and circle about a post, others frequently ranged themselves in line until they formed a ring, and presented much the appearance of a savage tribe in a dance. But, while the stamping of each ape was definitely heavier with one foot, there was no unison—only a tendency to keep time together. And there was nothing to show that the dancing followed any pattern—that there was imitation in the cultural sense, with social acceptance of a form. The dancing of one individual stimulated other individuals into analogous behavior; but the performance of each apparently remained a purely physiological response. When the gamboling of one lamb sets others to gamboling, or when one startled sheep runs and the flock follows, the sheep do

not possess culture because they follow one another's example. If one ape devised or learnt a new dance step, or a particular posture, or an attitude toward the object about which the dance revolved; and if these new acts were taken up by other chimpanzees, and became more or less standardized; especially if they survived beyond the influence of the inventor, were taken up by other communities, or passed on to generations after him,—in that case we could legitimately feel that we were on solid ground of an ape culture. But of this there is as yet no indication.

It is the same with chimpanzee fashions in smearing white paint, or teasing chickens, which Koehler describes. These are comparable to the vogue which a game or social manner or dress fashion has among ourselves; to the fact that the first boy who brings out his kite or his marbles in spring is almost certain to set other boys of his school to bring out their kites and marbles. What is cultural in such phenomena is not the fact that one individual leads and others follow, but the game or fashion as such. The kite, the manner of manipulating the marbles, the cut of a garment, the tipping of the hat, remain as cultural facts after every physiological and psychological consideration of the individuals involved has been exhausted. Of any such institutional residuum of unmitigatedly cultural material, there is as yet no demonstration among the apes.

THE USE OF TOOLS BY THE APES

When it comes to our third criterion, that of tools, the case is different. The anthropoids use tools; and they make them. Chimpanzees take up sticks to draw to themselves food which is beyond reach of their arms. They beat with sticks for the same purpose, or cast ropes or rope-like objects. If the desired food is out of reach overhead, jumping to reach it has led to failure, and there is no other individual about that can be climbed onto and used as a take-off for a higher leap, many of them finally have recourse to moving a box or other convenient object under the prize. If, after they have learned to use a box, the food is hung still higher, they learn to pile a second box on the first; and the more versatile ones will pile three or four. Gorillas will also do this. As Koehler justly points out, the piling of the second box on the first is psychologically a quite different thing from moving the first box; there is in it the element of combination, or construction. The difference is like that between rolling a stone and building with stones.

If the convenient reaching tool happened to be a bundle of straws, one chimpanzee, finding the straw too soft to move a banana, without hesitation stiffened the bundle by doubling it. Even then the tool was ineffective, so she redoubled it. That it was now too short to reach the banana rendered the result ineffectual, but does not detract from her credit as an inventor: she got the problem and knew what to do about it.

Especially interesting is the observation that two canes were joined one into the other to draw in food which lay beyond the reach of a single cane. This is indubitable tool making; especially when a stick is chewed down to fit into the hollow of a cane.

How far chimpanzees under proper stimuli might progress in devising tools for themselves is difficult to say; just as the observations leave it somewhat obscure how far slower-witted individuals tend to profit by the discoveries of a more inventive one. There are however some interesting observations as to the circumstances of the process of invention.

First, the chimpanzee strongly dislikes the strain of situations which call upon his inventive faculties. The process of invention is visibly and disagreeably arduous for him. His first impulse is to give up, or to become angry, if he cannot arrive at a solution by purely physiological means such as leaping or biting. Characteristic is the fact that if a reaching implement is in line of vision with the desired object, it is usually promptly utilized. If on the other hand, the stick lies behind the ape's back as he faces the food, it will not be "thought of" or noticed and taken up for a long time, when the experiment is a novelty to the animal being observed; in fact, usually not until after repeated renunciations and recurrences of desire. Emotions clearly are important, constituting a strong resistive factor. The individuals that meet difficult problems most readily, and carry invention farthest, are evidently those best able to control or inhibit the emotions which the prospective goal arouses in them.

COMPETITION AS A STIMULUS TO INVENTION

But emotions of another kind can be an impelling influence toward invention. These are the social emotions. His desire for affection, and for approbation from human beings, certainly helps a chimpanzee to invent tools. In the state of nature it is probable that competitive emotion—jealousy—is even more stimulating. Significant is Koehler's observation of the behavior of his adult female chimpanzee when a loaded box or heavy obstacle was placed to prevent her from reaching her food beyond the bars. She was perfectly capable of moving the obstacle; but the problem weighed on her for two hours. When however one of the young animals began to stray in the direction of the food, from which it was not separated by bars, she suddenly seized the heavy box, shoved it out of the way without hesitation, and grasped the prize out of reach of the competitor. Next day she found the solution in one minute.

The same chimpanzee objected to using sticks for reaching unless they were, so to speak, thrust into her hands by their placement. For half an hour she neglected a stick which was close behind her and which, as a retinal image, she saw whenever in aimless irritation she turned around. After a while she stood on the stick. She must have felt it with her sole; but again, as a personality, she refused to receive the sense impression. After half an hour a free chimpanzee came near the food. The jealousy which his approach excited was utilized to repress the sulking emotion hitherto displayed; and suddenly the ignored stick was perceived, seized, and used to draw in the food.

The one gorilla tested reacted less emotionally, but showed less inventive faculty than the cleverest of the chimpanzees.

These observations may not throw much light on the question of how far apes possess culture. They do however suggest much as to the psychology which underlies human culture, and what we are accustomed to term its progress. They indicate that the elimination of the competitive factor among men would deprive civilization of one of its principal and perhaps indispensable impulses. They suggest further why the institutions, codes, and ethics of all peoples have so strongly emphasized inhibition; why, for instance, courage—the repression of fear—has always been esteemed a high if not the highest virtue; and why, similarly, all social groups condemn incest. Not that the anthropoid apes set up moral standards. But all human groups do; they have evidently learned, on the basis

of individual life experiences, the social importance of restraints. The inference would be that from soon after the time when men began to possess institutions, and were able to formulate these in speech, they have never seriously swerved from an insistence on a social limitation of the natural sex impulse.

PLAY AS AN ELEMENT IN INVENTION

Play is evidently an important element in chimpanzee invention. Situations are often first met, or devices prepared, not from a desire to achieve a useful end, but as a matter of sport or amusement, as a means of satisfying pure manipulative interest; the utilization is later. Here again we have parallels with human culture. The lodestone or magnet was long a toy, or an object of pre-scientific marveling, before it was used in the compass and still later in machinery. The Chinese placed a compass on "south pointing chariots," where it could have served no purpose other than as a refinement of luxury, nearly a thousand years before they employed it in the serious business of navigation. They knew gunpowder in fireworks centuries before they put it into firearms. In fact, in both cases the Chinese play invention seems to have passed to other peoples, the Arabs and Mongols, to have been turned by them to more practical purposes, and then to have been re-introduced into China.

The domestication of animals, although its whole history is far from clear, appears to derive at least in part from the keeping of pets. To be sure, the keeping of a pet, which may be played with so long as it is amusing, and allowed to starve or escape when it becomes troublesome to maintain, is a different thing from the tiring business of continuously caring for flocks on which living depends. Also, of the numerous species of animals which are interesting enough as pets, many are of no economic utility, and others are incapable of being domesticated to the point where they can be regularly handled and fed and reared with economic profit. Still, it is clear that many primitive peoples who never rear either domesticated animals or plants do keep pets frequently. It can hardly be doubted, therefore, that a stage of play domestication preceded economic domestication of animals in the course of human history.

Among us occidental moderns the process of invention is difficult to understand; perhaps because we cannot yet sufficiently extricate ourselves from our own civilization to look upon its processes with the same objectivity with which we view those of foreign or ancient cultures. Nevertheless, one thinks of the pneumatic tire, first employed on the bicycle in the period when this was a novelty and instrument of sport, but gradually helping the motor car to develop into the important element which it now forms in our economic structure.

SCIENCE AS A FORM OF PLAY

Modern invention is of course completely interwoven with modern science. Now, time and again scientists have pointed out, sometimes when they were asking for money and sometimes when they meant what they said, that the progress of applied science or invention depends on the progress of pure science or discovery. Researches which, at the time they were made, could not have been conceived of as leading to practical results, have nevertheless again and again led before long to the invention of useful contrivances. The whole history of electrical discovery is a case in point. Now the significance of this, in the present connection, is that pure science is, after all, play. We are accustomed to think of

it as hard work because it requires intense specialization and long application. But in these qualities it agrees with modern sport. Like modern sport, it is, economically and physiologically, immediately useless. It is even more than useless: it is unnatural—a fact often charged against organized sport, but just as true of science. There is in us an element making us strive for mastery or excellence or perfection of achievement for its own sake, apart from the satisfaction of any definable physiological need. It is the driving of this impulse to the point of physiological discomfort, even of bodily strain or damage, that gives sport and science their quality of unnaturalness. At their fullest, they are perversions of the play impulse.

No chimpanzee seems capable of being so perverse: he is too unintelligent, from our point of view; but also too sensible, too concordant physiologically. For better or for worse, however, we men are prone to this exaggeration of the play impulse; and, again for better or for worse, the exaggeration has perceptibly aided the gradual accretion of the stock of modern culture, as well as the betterment of athletic records.

The chimpanzee, in his youth, is as playful, restless, curious, and explorative as any human being. He does not go very far in tool invention, because his central nervous system seems to become quickly and healthily fatigued by play which puts on the nervous system any strain that cannot be promptly discharged into striped muscle activity. He is physiologically a clear extravert. The gorilla, on the other hand, is described as an introvert, with more self-respect and sense of value of his personality. It remains to be seen whether in the field of pure intellect the gorilla will prove the equal or superior of the chimpanzee, once we have learned to establish relations with him satisfactory to his temperament.

A demonstrated psycho-physiological trait of the ape is lack of patience in the solution of a problem. As soon as difficulties are encountered which cannot be solved by direct use of hands, feet, or mouth, the chimpanzee tends to take refuge in irritation or sulks; the gorilla becomes dignifiedly indifferent. An added stimulus, such as doubling the reward, or approach of a competitor, may launch him again at the task, and perhaps with success. But the effort is new, not continuous.

The fact is of interest because it finds a parallel in the history of culture. There was required actually less skill to fashion many of the ground or polished stone implements of the New Stone Age than some of the specialized chipped ones of the Old Stone Age, tens of thousands of years earlier. The average modern person who has never worked stone would, if the reward were sufficient, almost certainly turn out on the first attempt a better ground mortar or ground stone axe than a chipped knife or spear point, if indeed he would not fail utterly in the latter. The reason is that while chipping requires definite manual control, it is a very rapid process. A dozen failures occupy little time; each may suggest the possibility of an improvement; and the thirteenth attempt may be reasonably satisfactory. Grinding, however, although one of the simplest of operations, is of necessity slow. Early man was apparently readier to mobilize a fair degree of manipulative skill than a great amount of patience.

INVENTION BY ACCIDENT

That the chimpanzee possesses a beginning of ability to reverse his primary impulse is shown by a series of experiments by Koehler. After the animals had learned to use a stick to gather in food from beyond their reach, the fruit

was placed behind a barrier, in a low open box with only the farther side broken out. To get his banana the ape had therefore either to lift it with his stick out over the front or side edge of the box, which was difficult; or he had to reverse his first impulse of scraping the fruit toward himself, and instead push it farther away until it was clear of the box; after which of course the familiar raking-in process could successfully commence. Without exception the apes found this problem difficult. Some never solved it except when the box was partly turned to help them; others only by the aid of accident, such as the banana rolling favorably; and even those who had learned the necessary reversal, tended to relapse into their earlier, direct, impossible efforts. Still, some of them did learn, and with practise came to perform quickly and efficiently. These results are a genuine credit to the more gifted individuals of the chimpanzee species. More observations as simple and significant as this are a desideratum.

This experiment developed a type of success which probably has its parallel in culture: invention partly by accident. The banana, prodded by the stick, rolls or bounces near an open corner of the box, or entirely clear of it, and the animal immediately sees a solution that had been beyond its grasp while the problem remained unmitigated. After this partial aid by chance, the whole problem is soon mastered.

Whether invention wholly by accident occurs in human culture, may be doubted. But that accident sometimes assists, is likely. At any rate, there are devices like the bow and arrow, and the fire-drilling apparatus, which seem to be by-products of other devices subsequently improved or converted when a chance variation suggested a new utilization. A bow which fails to attain a certain efficiency is of no use as a weapon. Yet an efficient bow is a fairly complex implement of delicate adjustment with which a first inventor would be almost foredoomed to fail. Its origin is best conceivable as a secondary stage of a bow used as a toy or musical instrument, which, being later produced with the requisite strength and balance, would be serviceable for propulsion. We do know from archaeology that the bow came into culture relatively late—not until the terminal phase of the Palaeolithic. The fire-drill is a simple apparatus but needs to be adjusted and operated in a particular way before a spark is obtainable. Drills used for boring, however, would sooner or later be likely to produce smoke or even a spark, and a new application be suggested. It would be rash to contend that any invention was ever due wholly to lucky chance. If there were no insight into problem nor recognition of need, the accident would pass unobserved and unutilized. But it does seem that previous accomplishment, plus insight, plus accident, have at times led to the creation of new cultural material. And the same three factors occur in chimpanzee invention.

The chimpanzee depends much more than we on muscular strength and gymnastic skill. Even the most intelligent anthropoids manifest little sense of statics. They pile three or four boxes randomly and then balance their own bodies to counteract the imbalance of the mechanical pile. Boxes are set on an edge or corner and the animal tries to mount them—in some cases succeeds because of its natural acrobatic capacity. The one gorilla tested proceeded more like a human being in adjusting and trying out the boxes; but this was a proportionally heavy animal, and without jumping impulses. Of course a solution which

depends for its effectiveness on muscular skill is in that degree farther from an invention in the cultural sense. An imperfect tool suffices; the congenital body makes up the deficiency. If men had the strength of arm and jaw of the great apes, their enormous canine teeth, they would no doubt have continued for a long time to meet many situations with muscle rather than with tools.

The impulse to perform with his body is strong in the cleverest chimpanzee; performance with a tool is usually clumsy and always an arduous act at first. Given a suspended banana and an available pole, the first impulse is to climb the pole before it can fall and grasp at the fruit—a sort of pole-vaulting. Sticks are brandished threateningly in play combat. But let a chimpanzee lose his temper, and he drops his stick and plunges into attack with hands and teeth.

Nevertheless some use of tools is spontaneous. Stones are hurled. Sticks are used to dig in play or for roots, to tease fowls or other animals, to touch fire, lizards, live wires, or other things that provoke both curiosity and fear. In removing filth from his body, the chimpanzee prefers a stick, chip, leaf, or rag, to his fingers. He will lick up ants, or hold out a straw for the ants to crawl on and then lick them off. He has not been observed, outside of posed problems, to manufacture tools or to lay them aside for the future; he does certainly, without human stimulation, use simple tools that come to hand, and use them in a way that in a human being we should call intelligent.

INVENTION AS A SYNTHESIS OR AS A COMPOSITE

Sometimes an ape sits down in front of a problem that has baffled him, detaches himself from his previous efforts, and looks the situation over, seemingly thinking. How far he may actually study the situation is difficult to say; but he certainly appears reflective. Suddenly then, sometimes, the solution comes and is applied without hesitation or awkwardness. Again, it may come overnight and without warning. When a human being acts in this manner we say that he has thought the problem out. At any rate the ape's solution tends to come as a whole, as an abrupt synthesis.

Now as we think of the course of human culture, it may seem as if the layman conceived of invention happening by syntheses like those of the chimpanzee, whereas the social scientist tended increasingly to view its history as one of gradual accretion. Both are correct. What we call an invention is normally a composite of many inventions gradually assembled. Each unit invention, however, probably depends on one insight made as a synthesis—a simple one, mostly, but a synthesis. Popular imagination, with its love of the dramatic and abhorrence of the analytic, transfers the process operative in the unit to the ensemble. It makes the printing press, the steam engine, the telegraph, the radio, spring like Pallas Athena in full panoply from the head of some human Zeus. As an explanation of what happened, this is pure myth. The steam engine, the telegraph, the automobile, are obvious composites. They function as cultural units, but the process of development of each totality has been a complex and slow one. An automobile represents literally thousands of inventions. Its hundreds of parts, like the screw and the cogs, have each its history of successive stages, each of which was in its time an invention. As Gilfillan has recently shown, the reputed inventor of every machine is regularly that individual among a number of contemporaries who first made a given assemblage of existing inventions pay. In

the eyes of the world successful invention is successful economic exploitation. And however we may rebel ethically or aesthetically, this verdict has primary culture historical validity. It is when a machine makes money that it comes into cultural use and consciousness. At the same time, a scientific interpretation of culture must penetrate deeper and recognize the antecedent stages and gradualness of development; much as for reckoning our ages we count from the day of birth, but the biologist in studying life history goes back of that act of emergence into pre-natal life, to conception, and beyond that to the ancestral germplasm.

It is the innumerable minimal unit elements of human invention that find their rudimentary prototypes among the anthropoids in their qualities of discreteness and synthesis. Beyond that, the parallel does not go; for the interrelation and accumulation of these elements is a cultural process, and culture the apes as yet give no indication of possessing.

THE DESTRUCTIVE IMPULSE

Left to themselves, chimpanzees are destructive. They love to demolish. Like small children who have grown up uncontrolled, they derive immediate satisfaction from prying, ripping, biting, and deliberately smashing. Once they begin, they rarely desist until an object has been reduced to its components. They never learn to lace shoes; they find spontaneous pleasure in unlacing them. The impulse to construct is infinitely weaker; it is called into activity only by special problems, and the solution of these is trying. One of the few exceptions is nest building. This the chimpanzee does from an early age, and apparently without being taught. Here we seem to have a genuine case of what in the older terminology was called "specific instinct." Nest building is of interest because directed toward an objective outside the body. But, according to both Koehler and Yerkes, the building is partly a drawing and tucking of branches under the body. Some of the twigs snap off and tend to hold in place the branches which remain attached to the tree. In this way a tolerable mat or platform is built up. This however remains, during the act of building, in contact with the ape's body; it is built against his skin, he feels it during the process of construction, and the sensations aroused may be an important element in the carrying out of the process. Some chimpanzees, if trees were not available or loose material did not suffice, laid down a ring that outlined the body and merely suggested the nest—a nest gesture, as it were.

The powerful impulses of chimpanzees toward destructiveness may help to explain one phenomenon in the history of human culture already touched upon: the long precedence in time of the chipping over the grinding technique in stone. After all, the earlier and grosser process of production by fracture is one of breaking apart. Grinding, being so slow as to be almost imperceptible in its results, must be quite unsatisfactory as a means of satisfying the demolition impulse. As an object is slowly rubbed into form, there is probably rather a sense of shaping and constructing. Of course, the Chellean picks and other early Paleolithic artifacts are not mere by-products of an interest in cracking boulders; they are too definitely adaptive, too patternized, too utilizable as tools. But preceding the Palaeolithic there are the "eoliths" which have been championed by some and denied by others as the earliest tools. They date back to the Pliocene, if not the Miocene, much beyond the earliest fossils of organisms in the line of human descent. It is gener-

ally admitted that the eoliths were not fashioned as tools but produced by natural agencies and then utilized as tools. Their finer fractures, usually confined to one edge, are interpreted as the results of wear during such use, and not as deliberate attempts to produce an edge.

In the light of ape behavior we can venture one tentative step farther. Our ancestors, like chimpanzees and children and human adults, probably took pleasure in demolishing. Learning among other things to smash boulders, and especially nodules of flint which long resisted and then shattered cleanly, they may have found themselves provided with attractively sharp and shining flakes, affording a new toy. Manipulation of these may have led to the discovery that the flakes furnished the possibility of a new satisfaction in hacking or scraping other objects. From such play in turn might have grown increasing habits of tool use; leading finally, when the mechanism of culture fixation and transmission became sufficiently developed, to the manufacture of tools as tools.

THE ORIGIN OF CLOTHING

We have a few observations that bear on aesthetics and religion. The apes are indifferent about being clothed or dislike it, although they appreciate a blanket in which to wrap themselves at night. On the other hand, they voluntarily drape themselves with strings and rags, wearing these for hours or days. The satisfaction is clearly in the wearing as distinct from the act of putting on. As Koehler aptly says, the heightening of bodily consciousness appears to be what gives the pleasure. Chains or strings which swish and sway with the motion of the body are favored; a girdle would probably be meaningless, or its presence be resented. The suggestion is that human dress for protection and human adornment spring from separate sources. This has long been good anthropological doctrine. However, in the history of man, protective clothing and adornment intergrade so extensively that a large class of phenomena can only be described as ornamental dress. Even basically utilitarian clothing is invariably affected by the fashion impulse in man. One may conjecture that there have been two developments little related in origin which secondarily came to overlap; and that dress and adornment, as we know them in the history of human culture, are largely hybrid.

RUDIMENTS OF AESTHETICS

Koehler's chimpanzees, in digging, discovered some white earth. Tasting it and finding it inedible, they spat it out. Wiping their lips, they saw the wall whitened. This soon became a game. First with their lips and then with their hands they painted with white earth whatever walls and surfaces were available; but rarely their own bodies. There was no attempt at design or figure. The stuff was smeared on, and the more the appearance of a surface changed, the greater the satisfaction. The pleasure apparently lay in using the muscles to produce a visibly effective external accomplishment. The act of creation gave satisfaction.

These observations accord with the behavior of small children, whose first attempts at what we are wont to call drawing or painting, even when an attempt is made to guide them, normally result in nothing more than smearing. It is rather evident that the small child, left to himself, does not attempt to draw a house or a dog or a man. He converts a white paper into a red or black one, a monotonous into a variegated surface. He defaces as much as he makes. It is

again demolition pleasure; or, more generically, the satisfaction of producing an effect; and this, at an early stage of development, is more readily accomplished by destruction than by construction. We tend unjustly to read the child as an adult. It is doubtful whether small children ever try to represent except as the result of cultural influence. In fact, we do not know that a human being become adult without impingement of cultural influences would try to represent anything. So too, when a child makes something like a decorative pattern, his principal satisfaction perhaps lies at first in the rhythmic motion. We, thinking primarily of the effect, are likely to construe into the child an impulse to decorative rhythm and regularity, which it probably does not appreciate until later in life. To understand art, it seems necessary to recognize that there is always a motor impulse involved; that in incipient stages the motor element probably predominates; and that recognition of aesthetic qualities as such is, historically, likely to be an overlay.

ANTICIPATION OF RELIGION

Religion is difficult to conceive without formulated ideas and thus without speech. Even its rudiments could therefore hardly be looked for among the apes. Yet there may be some sub-cultural anticipations. Koehler made a rude rag animal with shoe-button eyes which vaguely suggested a miniature donkey. It was altogether too crude to be mistaken for a live animal, yet had sufficient resemblance to one to set it off from ordinary inanimate natural objects, or from artifacts such as boxes or chairs. The apes responded instantly with manifestations of fear. It was not terror as great as an ox or a camel inspired, but can perhaps best be characterized as similar in its expression to what human beings would call awe. There was not a trace of either the indifference or the curiosity which a lifeless object provoked; interest there was, but also respectful staying at a distance for a long time. Even food placed in proximity to the image was shunned, and only at last cautiously snatched with a precipitate retreat ensuing. Koehler observed a dog manifest the same degree of interest in the figure, except that, being a carnivorous and therefore aggressive organism, his interest took the form of hostility. He convinced himself however, as soon as he dared, of the inanimateness of the image; and from then on was completely indifferent to it. The chimpanzee, like ourselves, is less practical, evidently as the result of possessing more imagination. Occasionally however, one of the lower animals will react more like a man or an ape. I have seen a young dog for weeks manifest panic whenever an imitation animal toy was brought into his presence.

The relation to religion of the chimpanzee's reaction lies in his manifesting something like the awe which is regarded as an important or essential ingredient of what we call the religious feeling: the religious thrill. It is generally recognized that religion could not well originate without the presence of emotions of which awe may be taken as the type; and that these emotions tend to persist, or to be re-awakened in religion, no matter how culturally crystallized this becomes. Also, the kind of object that arouses the awe-like feeling in chimpanzees has a certain quality of resemblance to the basic concepts of religion. Souls, ghosts, spirits, like stuffed rag donkeys, do not occur in ordinary experience; like them, also, they are thought to be at once similar to living bodies and different from them. A dummy donkey with button eyes evidently is literally supernatural to

a chimpanzee. We can then say pretty positively that the ape does not have a religion; we can also say pretty positively that he acts at times as if he were religious.

When we put together the observations and interpretations just reviewed, it becomes clear that we have in the anthropoid apes beings remarkably close to ourselves. They are animals behaving in innumerable respects like men and differently from all other animals. Faculties which we are accustomed to regard as specifically human prove again and again to be present in them in rudimentary form. What they do lack totally, so far as we can yet judge, is speech and culture. In this regard they are as sub-human as the other mammals and the birds. This is really remarkable in view of their possessing some of the ingredients universally accepted as going into the makeup of culture: especially inventiveness. The ape will not only use tools, he will not only make them when he is taught, he will invent them. That the tools are simple and crude is expectable; that he can and does devise them makes us wonder why he did not pass on to develop an elementary culture. The absence of speech undoubtedly is an important factor in this deficiency. This lack of language faculty has been ascribed to a lack of imitativeness as regards sounds. This lack may be granted; yet one cannot help but feel that it is not a wholly sufficient explanation. Similarly, it seems doubtful whether lack of speech alone is sufficient to account for the total absence of culture. It may well be so; but it will require further experiment, or at least much more extensive observation, before we may be sure that there exist no other potent factors of deficiency.

IS INVENTION THE CHIEF FACTOR IN CULTURE?

With the ape inventive but cultureless, the question arises whether we have not perhaps hitherto exaggerated the importance of invention in human culture. We are wont to think of it as the creative or productive element in civilization. We tend to view the other processes in culture as essentially those of transmission, preservation, or decay. The idea of progress, which has so powerful a hold on the unconscious as well as the conscious thought of our day, may have led us to overemphasize the rôle of invention. Perhaps the thing which essentially makes culture is precisely those transmissive and preservative elements, those relational or binding factors, which social scientists have indeed occupied themselves with, but have been inclined to regard as after all of secondary importance in comparison with the dynamic phenomenon of invention. It may be that invention will prove to be what is incidental in culture; that it is merely a fashion of our day to look upon it as primary. What may ultimately be recognized as counting for more is the way the patternings of culture shape themselves to permit or prevent or induce invention, or, for that matter, any change of civilization. This shaping of patterns is in another aspect a matter of interrelations of culture material; and what appears to be indispensable for such interrelations to exist is a certain social relation, an organization, or form, or almost a standardization. The fundamental thing about culture then would be the way in which men relate themselves to one another by relating themselves to their culture material. This is perhaps not so far from the basic concept which Durkheim was trying to formulate when he succeeded in expressing himself in a manner that seems somewhat mystic. It must be admitted that the present formulation too is lacking in precision. But it is difficult to see with clarity into the murky area that lies on the edge of or beyond what we actually

know, in the region where we apprehend rather than understand.

If however the relational forces in culture phenomena are the intrinsic ones, then the indispensability of speech to the very existence of culture becomes understandable. It is the communications, perhaps, more than the thing communicated, that count. At any rate the fact that speech, to the best of our knowledge, is as thoroughly wanting among the anthropoids as is culture, tends to confirm this conception.

CONCLUSION

There is a residuum of new understanding which knowledge of the apes contributes to knowledge of human culture. We see above all the tremendous influence of the play impulse. We see the unit elements of invention sometimes made with the aid of favorable accident; more often occurring as a product of reflection, of a kind of synthesis which in ourselves we call ideation. We see, perhaps a little more clearly than before, the relation of these unit elements of invention to the course of invention; and how culture, in its operations, fixes and settles upon certain patternized combinations of these elements. It is these combinations, as combinations, which it allows to enter into its consciousness and deals with. We see also that the impulse of destructiveness has probably played at times an ultimately constructive part in culture development. We are able to recognize more clearly the rôle of the emotions with reference to culture, and of it toward them. Inhibition of direct and primary emotional impulses is a necessity for culture to acquire material with which it can build; and the existence of inhibitions has been felt by all cultures as indispensable to the preservation of themselves and of societies. On the other hand, emotion is also a positive factor. Competitive feelings in particular seem culturally stimulative; and we gather at least an inkling of the part played in religion by awe.

Many or all of these conclusions have at one time or another been reached tentatively or positively by anthropologists from the examination of human culture itself. The study of the anthropoids, however, yields grateful and valuable corroboration. Cultureless these higher primates are; but with reactions and faculties closely akin to our own, and manifesting at least some measure of the basal psychic ingredients which enter into culture. There is infinitely more to be learned from them by wise experiment, and no less by critical observation. We have only begun. In fact, with the wide interest in these animals, it is surprising how scant the significant scientific data on them as yet are. Further study of them is important in itself; it will be invaluable in the illumination of the basic problems of anthropology and all the social sciences; and will in turn be furthered by what it can derive from these sciences.

LIST OF LITERATURE

Yerkes and Child, in a late number of this JOURNAL (2, pp. 37–57, 1927), have reviewed recent contributions to knowledge of anthropoid behavior and given a bibliography which makes a formal list of literature unnecessary. References here are by their numbers. The work of basic importance in the present connection is Koehler, The Mentality of Apes (47), a translation of the original (41) and (45). In (43) Koehler discusses some of the culture anticipations here considered. He seems to share my view that the anthropoids cannot be credited with culture. Very valuable are Yerkes' contributions (78), (79), (80), (81), plus two subsequent papers, The Mind of a Gorilla (Pt. 1 and Pt. 2, Genetic Psychology Monographs, Clark University, 2, nos. 1–2, 6, 1927). The latter of these two came to my knowledge after the present

essay was written and has not been used. Kohts's studies (48), (49), have not been accessible to me except through Yerkes' abstracts. They are rare in this country, are in Russian except for a German summary of (49), and evidently deserve to be translated in full. On the subject of language, Boutan (13), Furness (29), and Yerkes and Learned (81) are conclusive. Learned's portion of the latter is an objective record of chimpanzee utterances, probably accurate as to pitch but inadequate in other phonetic aspects. It is to be hoped that a phonetician can be interested in the subject. Similarly, on strength, Bauman (10), (11) has opened a subject which should be followed farther. Boutan's work (14), on mechanical problem solving by human children, brings in also anthropoid observations, and is marked by acuity and clarity of conception. Brehm's Tierleben in its last edition, edited by Neumann, (16), (17), reviews or quotes many of the older accounts, which are often extremely illuminating. As regards Garner, I concur with Yerkes: he knew his primates but misunderstood them.

ROOT HAIRS AND GROWTH

By CLIFFORD H. FARR

Henry Shaw School of Botany, Washington University, St. Louis, Mo.

WHY STUDY ROOT HAIRS?

GROWTH is the most complex of all biological processes. It is, indeed, a resultant of all of the physiological processes: absorption, synthesis, assimilation, conduction, digestion, respiration, and secretion. Any circumstance which affects any one of these physiological processes is likely to affect the rate or the type of growth. Thus the increased absorption of a substance may increase the rate of growth; or, on the other hand, it may retard growth, according to the kind of substance and the state of the organism. In general if the processes that tend to build up the organism, such as synthesis and assimilation, occur more rapidly than the processes which tend to tear it down, such as digestion and respiration, growth will occur. Growth may therefore be looked upon as the net result of physiological activity. It is a sort of index of the well being of the organism as a whole.

Growth however is not to be looked upon as the sum of all of the physiological processes. They are to be regarded more or less as aspects of the activity of the organism as a whole. Growth on the other hand is fundamentally a cellular phenomenon. While its rate is determined by the resultant of the physiological processes, it is itself a combination of cytological processes. It embraces, in fact, three phases of cell activity: division, enlargement, and differentiation. Cells undergo development in three ways. They divide, they enlarge and they differentiate. By differentiation is meant the change of an embryonic cell into a tissue cell. This change may consist in an alteration of form, composition, or content. It may mean the appearance of new organs, such as plastids, vacuoles, and so forth. It may, on the other hand, mean the disappearance of the nucleus, as in certain of the blood corpuscles or in sieve tubes; or the entire protoplasm of the cell may die and decompose, leaving only the thickened cell wall, as in certain of the plant fibers or conductive vessels.

We may, it is true, determine the growth of an organism by determining its increase in size or weight. Especially in the case of plants the increase in size or weight of only a portion of the organism, as the fruit or tops, may be taken; or it may be only of a portion of the constituents, such as dry matter or ash. By obtaining such data we can ascertain the effect of certain external conditions upon the state of the organism as a whole, without analyzing its effect, as to whether it stimulates or retards absorption or assimilation, etc., or as to how it affects cell division or enlargement or differentiation.

It is apparent that while such studies are useful in increasing our knowledge of the effect of external conditions upon crop production and such practical considerations, they cannot go far in extending our

understanding of the fundamental nature of growth. In order to understand the physiology of the plant or animal it is necessary to place it under as nearly constant conditions as possible, and then to vary one condition and measure the effect of this change upon one process as nearly as possible. In like manner, in order to study the growth of an organism intimately, it is desirable to proceed in the same way, noting the effect of the change of one external condition upon one of the cytological processes of cell division, cell enlargement, and cell differentiation.

The past fifty years have witnessed a very intensive study of the mechanism of cell division, beginning with the work of Strasburger and Flemming. The study of nuclear division has been especially thoroughly prosecuted, largely because of the connection which has been established between it and the study of the transmission of hereditary characters. But we are still a long way from understanding how hereditary factors bring about the characters of the organism during its individual development, largely because we have neglected the study of the other phases of growth. We have not as yet determined how it is that conditions determine the plane of partition or the rate of cell division, cell enlargement, or cell differentiation. In order to do this it is desirable that cells be chosen which undergo essentially only one of these three processes to the almost entire exclusion of the others, and which can be studied while growing normally under constant and controlled conditions.

In the study of cell division this ideal can be almost realized by the use of bacteria and other microörganisms in which there is little differentiation or cell enlargement, and in which the rate of cell division can be measured by counting the number of cells from time to time. But there is such a wide gap between the cell of the microorganisms and that of the higher plant or animal that it is doubtful whether we are at all justified in applying the conclusions from the one to the interpretation of the other. The nearest approach to a satisfactory study of the effect of conditions upon the rate of cell division in higher organisms is by the method of tissue culture. This is, however, open to the criticism that the cells doubtless behave entirely differently in these cultures, than they do in their normal relation in the organism.

A much more satisfactory study can be made of the effect of external conditions upon cell enlargement through a study of root hairs. These are projections of superficial cells of the roots of plants. They are normally cylindrical in form, and enlarge only by elongating. A measurement of increase in length gives us a means of directly calculating the increase in volume of the cell, and hence its enlargement. The root hairs are produced, even, upon very young seedlings. This makes it possible to study root hair elongation while the entire plant at that stage is intact. The root can be allowed to extend into a moist chamber, or into a vessel of solution on the stage of the horizontal microscope. In this way we can have the plant under normal and controlled conditions and measure accurately its response to different factors of the environment in terms of cell enlargement, withoutcomplicatingcircumstances. The nucleus of the root hair does not divide, neither is there any other evidence of cell division occurring within the cell. The process of cell differentiation is reduced very nearly to a minimum. It here consists of an extension of the cell wall and an enlargement of the vacuoles incident to cell enlargement. There is probably a slight change in the composition of the

cell wall, but there is normally no thickening of the wall, nor any apparent differentiation of structure or substance within the root hair during its elongation.

Not only are root hairs desirable objects for use in the study of cell enlargement, but they also afford one of the most accurate means of ascertaining the biological effect of various physical and chemical agents. They can be readily exposed to different types of light and other radiations. Experiments can be arranged so that temperature can be accurately controlled and its effects investigated upon a cellular basis. Root hairs can likewise be subjected to various types of electrical phenomena.

It is, however, in the realm of chemical agents that they lend themselves to the greatest diversity of experimentation. The chemical substances which may be presented to roots of plants may be classified into four groups according to their effect upon the plant. They are either nutritive, that is, actually utilized in the construction of necessary organs and compounds; or they are toxic, that is, they have an injurious effect upon the rate of plant processes or cause abnormal development; or they are stimulating, that is, they accelerate plant processes above the normal; or they are neutral, that is, have none of these effects.

Root hairs are especially well adapted for the study of the biological effect of chemical elements and compounds, in that they grow either in air, so that gases may be studied, or in solutions, so that inorganic and organic soluble compounds may be used. The only element that is necessary in addition to those in water is calcium. Therefore they can be grown in so simple a solution as calcium hydroxide. Other soluble substances can be studied by adding them to calcium hydroxide, and hence having them in a very simple solution. In this way the various nutritive, toxic, and stimulating agents can be thoroughly studied as to their biological effect in various concentrations and under various conditions of light and temperature and of degrees of acidity and alkalinity of the medium.

In studying these chemical factors it is obviously advisable to investigate the nutrient constituents first. Only after they are completely understood can we hope to make a careful analysis of the stimulating and toxic substances. We know that certain elements, namely, nitrogen, potassium, phosphorus, magnesium, iron, sulphur, and calcium are actually utilized in the construction of plant tissues. These are certainly to be regarded as nutrient elements. Certain others, such as sodium, chlorine, manganese, and boron seem to be present in most plants, and may eventually prove to be of direct nutritive value.

The study of the nutrient constituents of plants began with the chemical analysis of wild plants and of the soil upon which they grow. As the science of chemistry has developed this study has become more and more intensive and extensive. The study of cultivated crops and fields was undertaken in the same way with more dependable results because of the more uniform conditions. If such investigations were made in experimental plots especially planned for this purpose still more consistent data were obtained. A further improvement consisted in growing the plants in greenhouses in benches, flats, or pots, where temperature and humidity could be somewhat controlled. But even here the complexity and variability of the soil made definite conclusions very difficult. A very important advance was then made by growing the plants in sand to which nutrient elements were added in the form of simple inor-

ganic salts. Still better results were obtained by using solutions in jars, so that the roots were not in contact with any solid substratum at all. In this case it is necessary to supply the roots with oxygen by bubbling air through the culture solution from time to time. It was also found that the composition of the solution changes rapidly owing to the absorption of some substances from it more rapidly than others, and the liberating of substances, especially carbon dioxide from the root. This difficulty may be overcome by an elaborate system of growing the plants in a flowing solution.

But even this most refined method of studying the balanced rations of plants has not given as conclusive results as are desired. One of the difficulties consists in the long period of time required to raise the plants to maturity, even in these solution cultures. So many things may occur during the course of several weeks which may have an effect upon the final results, that it becomes somewhat uncertain just what to attribute to the effect of the one element which is being studied. In order to raise plants to maturity there must be present in the solution at least seven mineral elements. This means at least three or four salts. To discover the specific effect of each of these elements then becomes a problem, because of the interactions which are known to occur between them. Finally there is the difficulty of finding an exact criterion of the degree of development of an organism such as one of the higher plants. As noted above increase in size, weight, dry weight, etc. are the resultant of so many processes, and are in addition affected by so many external conditions, such as disease, insect activity, light, etc. that their value as a a basis for judging the well-being of the plant is seriously impaired.

There is need then for a new method of investigating the effect of the respective nutrient elements as well as the toxic and stimulating factors in the environment of a plant. It seems that a study of cell enlargement of root hairs affords a logical opportunity to do this, inasmuch as they are in part, at least, the absorptive organs of the plant. As noted above, the history of the study of the balanced rations for plants represents a series of progressive simplifications of conditions surrounding the experiment. First plants were studied as they occur in nature. Then they were placed as nearly as possible under the same conditions as far as soil was concerned. Next wind and many animals were shut out, and the temperature and humidity of the air were held more constant. The next step was to exclude the organic matter of the soil; and following that the entire solid matter of the soil. Finally the gaseous and mineral content of the medium was controlled and kept rather constant. It is now desirable to simplify the experiment still farther by confining the study to just one of the phases of growth, such as cell enlargement, studying as far as possible each of the nutrient elements individually, before putting them together to form a balanced solution. Furthermore there is the desirability of studying the plant during a shorter period of time, during which light will be unnecessary, and the temperature, and acidity or alkalinity of the medium can be kept more constant. The study of the rate of growth of root hairs affords this opportunity.

We can determine first the rate of elongation of root hairs in different concentrations of calcium hydroxide. Inasmuch as this is a basic compound, increasing the concentration means also increasing the alkalinity of the solution, so that, when we have studied different concentrations of calcium hydroxide we have also studied

different degrees of alkalinity. We can next use a neutral solution of calcium nitrate of different concentrations. This contains calcium ions (Ca) and nitrate ions (NO_3). By adding calcium hydroxide to calcium nitrate we can study the effects of different degrees of alkalinity for different concentrations of calcium nitrate. In this way we can obtain a rather exact idea of the specific effect of the nitrate ion (NO_3) and of the hydroxyl ion (OH). By adding nitric acid, HNO_3, to calcium nitrate, we can study the effects of different degrees of acidity for different concentrations of the calcium nitrate, and in this way obtain information regarding the effect of the hydrogen ion (H). This same method can be repeated with calcium sulphate, $CaSO_4$, and calcium phosphate, Ca_3PO_4, thus obtaining a knowledge of the effect of the three nutrient anions, nitrogen, sulphur, and phosphorus, and also of one cation, calcium. The other three most important nutrient elements, potassium, magnesium, and iron, are cations. It is therefore necessary that they be studied by mixing their salts with those of calcium, inasmuch as calcium is necessary in order for root hair elongation to occur. We shall therefore have to study a solution of calcium nitrate, $CaNO_3$, and potassium nitrate, KNO_3, in different proportions, different concentrations, and different degrees of acidity and alkalinity. In the same way we can study magnesium nitrate, $MgNO_3$, and ferric nitrate, $Fe(NO_3)_3$. By studying the sulphates and the phosphates of these compounds in the same fashion, and then combining them in different ways, we can gradually build up the balanced culture solution with a thorough knowledge of the specific and mutual effects of each of its constituent parts.

It is therefore important that a study of root hairs be conducted intensively and extensively, in order to increase our knowledge of the nature of cell enlargement as bearing on the general problem of development, and from the standpoint of our knowledge of the biological effects of the respective nutrient, toxic, and stimulating features of the environment of the plant, especially of its roots.

THE FUNCTION OF ROOT HAIRS

Root hairs do not ordinarily occur over the entire surface of the root. The terminal portion of the root, consisting of the root cap and the regions of cell division and cell enlargement, does not bear hairs. Also the older portion of the root, that is, the part nearest the stem, is usually devoid of hairs. In fact in most roots the hairs are confined to a region between one and four centimeters in length near the tip of the main root and of the secondary roots and their branches. The hairless tip is usually of somewhat less extent; and, aside from the root cap, a protective structure which covers the tip, it is a region of growth, giving rise by cell division and cell enlargement to the region of root hairs above. By virtue of this elongation of the cells in the upper part of this region of growth, the tip of the root bearing the cap is pushed farther and farther into the soil. The region of root hairs is for the most part a region of cell differentiation. In it the surface cells produce protuberances which become the root hairs. The interior cells, on the other hand, become differentiated into the various cells of the older portion of the root, such as conductive cells, storage cells, etc. It is thus in this region of root hairs that the conductive tubes of the root, which are continuous with those in the stem, terminate as we follow them down the root, or originate as we trace them toward the stem. By virtue of the fact that the region of root hairs is being

added to by the region of growth below and in turn is giving rise to the older portion of the root above, it is a region which is migrating progressively farther and farther into the soil. Continually the root is adding new cells which give rise to root hairs in the lower portion of this region, while the older root hairs in the upper portion are collapsing and being sloughed off. The region thus presents a series of root hairs, gradated according to length, with the shortest near the distal end and the longest at the proximal end. The root hairs are thus usually short-lived structures, being formed by continuous elongation for a few hours, and then, after growth ceases, in most cases collapsing and being sloughed off in a few days.

There are, however, some exceptions to these rules. Cowles reports (7) that the prickly pear cactus, *Opuntia*, has root hairs to the extreme root tip. McDougal (52) has found them persisting over 15 or more centimeters of the root length of certain woody legumes, as the honey locust, red bud, and Kentucky coffee tree, for a period of several months. It is likely, however, that these hairs persist upon the root for some time after they die. He reports that in all except the younger stages they are thick-walled and brown in color and about four times their typical diameter. These root hairs, then, unlike those of most plants, undergo some cell differentiation, as well as elongation. McDougal correlates the persistence of root hairs in these plants with absence of root nodules. Miss Whitaker (86), however, found persistent root hairs in other groups than the legumes. She correlates this habit with a suppression of growth of the root in diameter. In a number of the Compositae, as asters, golden rods, dahlias, chrysanthemums, etc., she found them persisting even for two or three years.

The function of root hairs has been the subject of discussion ever since they were first figured and described in the latter part of the seventeenth century by Malpighi (50) and Grew (28). These two botanists, the one an Italian and the other an Englishman, laid the foundations for plant anatomy. They both found the root hairs and studied them in a general way; but they differed in their opinions regarding their function. Malphigi thought that they were the organs of absorption of the plant; while Grew considered that the plant absorbs through its tip, especially through the root cap. From this time on, for a century and a half, botanists differed upon this point. Their evidence regarding it was conflicting, owing probably to using different kinds of plants and to inexact methods of experimentation.

In 1837, however, Ohlert (57b) performed experiments which seemed to be conclusive. He used peas, lupines, and marigolds, cutting off the hairless root tip and covering the wound with lacquer. He found that the plant grew normally, showing that the root absorbs through the lateral surfaces upon which the root hairs were disposed. Meyen (56) in the next year concluded that the root hairs were the organs of absorption of the plant. He pointed out that they increase the surface of the root and extend the area of absorption. This conclusion has been accepted almost without question by the leading botanists to the present day. Persecke (62) thought that they were able to condense water from saturated air and absorb it. Mer (54) in 1880, however, showed that they must be in contact with liquid water in order to absorb it.

In 1883, Schwarz (73), who made the first extensive study of root hairs, considered their function more intimately. He calculated that they increase the surface of the root from 5.5 to 18.7 times

according to the species studied. It would therefore seem that by increasing the surface of the root they increase enormously its ability to absorb. However, this deduction of Schwarz should not be taken without more careful consideration, as it is very easily misconstrued. It is likely, in fact, that they do not increase the capacity of the root to absorb water at all. All of the water absorbed must enter the root proper through the base of the root hair, and since the walls of the surface of the root are apparently perfectly permeable to water, no more can pass into the root proper through the base of one of these hairs than could enter through the same area if no root hair were present there at all. That is, a root immersed in water can probably absorb no more water by virtue of its root hairs than it could absorb if it had no root hairs at all. The advantage of the root hairs in the absorption of water is, however, that in the usual situation in the soil, they extend out and come into contact with supplies of water which would not otherwise come into contact with the root at all. They therefore increase its ability to obtain water from a more or less dry soil, though they do not, apparently, increase its total capacity to absorb water.

With regard to salts, the root hairs doubtless have the same advantage of extending to new supplies of the salt not otherwise accessible; but they also probably actually increase the amount of salt absorbed due to the increased surface. This is due in part to the fact that the cells are not perfectly permeable to the salt, and hence more can enter the root through the base of the hair than could enter through that area devoid of a hair. There is also the effect of protoplasmic streaming to be considered in connection with salt absorption. As will be shown below the protoplasm in most, if not all, root hairs is in a state of circulation to and from the cell proper. This means that once a molecule of salt enters the cell it is likely to be quickly carried into the cell proper, thus giving opportunity perhaps for additional absorption of the same salt by the root hair.

However there have been a few studies from time to time which seem to raise a question as to the absorptive function of root hairs. Mer (53) raised the question in 1879, but presented no definite evidence bearing on the point. Frank (26) in 1887 determined the location of absorbed KNO_3 by staining roots in diphenylamin-H_2SO_4 after they had been growing in a solution of the nitrate. He found it in the region of elongation upon which no root hairs had been developed. Kny (40) repeated the experiments in 1898 and obtained the same results for aqueous media, but he points out that in the soil the reaction occurred in the region of root hairs since they extend nearer to the tip in the form used. Overton in 1902 found that root hairs of *Hydrocharis* are plasmolyzed in most, if not all, inorganic salt solutions and hence he concluded that they do not absorb. Coupin (6) in 1919 found that roots grew about twice as fast when only the tip was immersed as when the entire root was under water. But he does not preclude the absorption of water condensed on the root hair in the saturated atmosphere above the water in the first case, nor does he demonstrate that there was an adequate oxygen supply for the entirely immersed roots. In a later paper he contends definitely that not only does the root tip absorb, but also that the root hairs do not absorb. However, he does not present evidence which is convincing in this regard. Turina (80) worked with salts which he found were absorbed from the solution and deposited in the root cap

and in the region of cell division. This has been taken as evidence that they entered directly at this point. Priestly and Tupper Carey, on the other hand, have studied the chemical composition of the cell wall in the root tip and find that it contains proteins and fats or fatty acids. These they regard as the substances which render these cells impermeable, or at least, not freely permeable to water. Dissolved substances may, however, enter these cells and hence they are able to divide, whereupon they may take up water and become cells of the region of elongation.

Recently Popesco (64) has presented an extensive study in which he attempts to discover just which region of the root does absorb. His method consists in placing the roots in solutions of dyes, such as eosin, neutral red, and methylene blue and noting the parts which become stained. He also covered different parts of the root with cacao butter and noted the rate of absorption of water and of dyes. Finally he impregnated the root with potassium nitrate or iron sulphate by allowing it to grow in a solution of one or the other of these compounds and then sectioned and stained it so as to detect where the nitrate or sulphate was located. He concludes that plants absorb water from a solution just as rapidly if they have no root hairs as if they are well supplied with them. He finds that the root does not absorb through the root cap, but that the region of absorption bears a definite relation to the internal structure of the root. That is, it is located in the vicinity of the lower ends of the conducting tubes, rather than being defined by the location of the superficial root hairs. It usually happens, however, that these two regions are somewhat the same, that is, the tubes usually end in the vicinity of the region of the young root hairs.

From his work it would seem established that the surface of the root in the region of root hairs and immediately below it, that is, in the region of cell elongation, is as readily permeable as are the root hairs. However, it does not seem that he has demonstrated that root hairs are not absorptive organs. In the first place it must be borne in mind that much of his work is based upon the penetration of dyes and not of water. In the second place his study shows upon his own criteria that in many cases, the younger root hairs especially do absorb. Furthermore from the results of experiments to be described below, it is doubtful whether he has given proper attention to the effect of immersion in a solution upon the growth of root hairs already formed, frequently causing a cessation of elongation, and to the production of new hairs after immersion.

That root hairs actually do absorb salts is shown by the interesting experiments of Osterhout (59). He found that when root hairs are immersed in a calcium solution and observed with a microscope equipped with a Nicol prism, crystals are seen to form in the root hairs. These crystals he identified as being of calcium oxalate. It is thus apparent that the calcium ions have entered the cell and combined with the oxalate ions present there in solution in the form of oxalic acid or potassium oxalate or some other salt, and that there has resulted a precipitation of the insoluble calcium oxalate in the form of crystals.

This point is borne out by the common observation that when seedlings are transplanted from a hot bed to the field, for instance, it is necessary that they be shielded from sun and wind for perhaps 24 to 36 hours in order to avoid wilting and possibly the death of the seedling. Inasmuch as about this length of time is required for the root to develop a new com-

plement of root hairs, it seems reasonable to conclude that under normal conditions the root hairs are of immense importance in supplying the plant with water.

Schwarz (73) also pointed out that root hairs have another function in addition to absorption, namely, anchorage. They secrete material which dissolves the surface of solid bodies in the soil, forming a cement which fastens them firmly to these soil particles. In fact, if a plant is pulled from the soil, the root hairs will either bring the soil particles to which they are attached along with them, or they will separate from the root, but not from the soil particles. It therefore appears obvious that they have a function in anchoring the young seedlings. They could have no such function in anchoring the older plant, inasmuch as branching of the root system and root contraction performs this so much more effectively. In the young seedling this function of anchorage of the root hairs is very important. It is not so much that it prevents the plant from being pulled out of the ground. Such a circumstance is a relatively uncommon experience. It does however prevent the soil from being completely washed away from the seedling in case of watering or of hard rains. But it has a still more important relation than this. It prevents the seedling from pushing itself out of the ground. The region of cell elongation is just below the region of root hairs. It is that region in which the cells elongate parallel to the axis of the root, and push the root tip into the soil. In pushing the tip into the soil, the latter obviously encounters resistance. The exertion of a considerable pressure is therefore necessary. Were it not for the root hairs which bind the region above to the soil, the exertion of this pressure of elongation would result in the upper part of the root being pushed up out of the soil, instead of the lower portion being pushed down into it. This is then the most important, because it is the most frequent anchoring function of the root hairs.

Hill (34) has pointed out an additional function of the root hair, namely that it is able to adjust the absorbing surface of the root to the concentration of the soil solution. The latter is likely to become greater as a result of evaporation of water from the soil, or to become weaker owing to rains or leaching. It is therefore desirable that the absorptive cells be newly formed from day to day to cope properly with these changing conditions. The progressive elongation of the individual root hairs, the progressive formation of new root hairs, and the migration of the root hair zone, accomplish this adjustment in an admirable manner.

STRUCTURE AND COMPOSITION OF ROOT HAIRS

Meyen (56) in 1838 was the first to give an accurate description of the structure and development of root hairs. According to Schwarz (73) they vary in maximum length in land plants from 0.24 mm. in *Vicia* to 3.25 mm. in *Tradescantia*. In aquatic plants they may attain a length of 5 mm., as in *Potomageton*, and of 8 mm., as in *Trianea*.

It is thus seen that a teleological explanation of their existence will hardly do; that is, we cannot say that a plant has root hairs because it needs them in order to absorb or to anchor the plant, inasmuch as the plants having the longest root hairs are those which need them neither for anchorage nor for absorption. On the other hand it is to be noted that the duckweed, *Lemna*, a free floating aquatic, does not have root hairs at all; while *Elodea*, a submersed aquatic, has them only when the roots are in contact with mud.

The question arises as to what cells of the outer layer of the root produce root

hairs. Leavitt (46) reported in 1904 that in the grasses every cell may produce a hair. In *Azolla* (45), a water fern, he finds that root hairs arise only from short cells. This latter observation was also made by Savageau (68) upon *Naias* and by Kraemer (41), Van Tieghem (82) and Juel (37). Schwarz (73) and Miss Snow (75), however, think that there is no significance in the size of the mother cells. Schwarz gives the diameter of root hairs as varying from 0.011 mm. in corn to 0.050 mm. in *Trianea*. He estimated the number per square millimeter of root surface to be 10.9 in *Trianea* and 425 in corn, and the number per millimeter of root length to be 94 in *Trianea* and 4386 in *Scindapsis*.

Haberlandt (29) in 1887 was the first to show definitely that the root hair grows in length by the formation of additional wall only at the apex, although Nägeli in 1846 had included plant hairs along with pollen tubes, fungous hyphae, and algal filaments, as structures with apical growth.

As to the exact method of cell wall elongation there developed some difference of opinion. Wortman (88) in 1889 contended that it was by the addition of new layers on the inside of the wall at the tip, and a stretching of the wall simultaneously by increased turgor of the protoplast, keeping the wall at a constant thickness, but increasing progressively the volume of the cell. Zacharias (89) in 1891 obtained strong evidence that this is not the method, but that new wall material is inserted into the wall at intervals along the dome shaped tip, thus extending the wall, and that turgor of the cell is not the active factor in cell enlargement. This idea has recently been supported by the work of Ursprung and Blum (81) in 1921.

The most convincing evidence that the root hair does grow at the tip only is given by the experiments of Reinhardt (65) in 1892. He placed minute particles of red lead on the tip of the hair and watched their change of position as the hair grew. He found that they might become subdivided on the dome-shaped tip and invariably moved off of the dome as the hair grew, coming to rest on the side of the hair at the base of the dome, and remaining in contact with this part of the wall, while there was progressively more lateral wall added from the dome at the end.

Stiehr (77) in 1903 found several lines of evidence which indicate that the wall of the hair at the tip is different in composition from that of the rest of the hair. He found that it is more readily stretched and broken, as is shown by the fact that if the root hair is caused to burst the rupture occurs almost invariably at the tip. He also noted the form of the tip when particles were appressed to it, and describes it as appearing in this respect like a stick of warm sealing wax.

On the basis of his experiments on the curvature of root hairs in response to certain stimuli, as described below, Seidel (74) concluded in 1924 that the wall is more plastic at the apex of the root hair than at other points. This would perhaps be expected if the apex is the place where new wall material is being deposited. It is also in harmony with the work of Ziegenspek (90) in 1920, in which he found that the cell wall at the tip is of different chemical composition from that along the sides. He decided that it consists of a substance, called amyloid, which is a transitional carbohydrate, having some of the properties of starch. For instance, it turns blue with iodine, as does starch; whereas for cellulose to give this reaction acid must be added.

However it is not entirely certain that

in this case the amyloid is to be regarded as an intermediate carbohydrate between the soluble form in the cell sap and the cellulose of the fully developed cell wall along the sides of the hair. Miss Roberts (66), it is true, in 1916 reported that there was an inner layer of cellulose along the sides of the root hair, the outer layer of the wall being of calcium pectate. However, in 1921 Miss Howe (35) published a further investigation of the composition of the cell wall of root hairs in which she found no cellulose at all. In this way the root hair wall is strikingly different from that of partition walls and other external walls of the root proper. She also found that the outer layer of the lateral walls of the root hairs is of calcium pectate or pectose, but that the inner layer is of callose, which Miss Roberts found only at the tip of the root hairs of some species.

Considerable attention has been given the question of the location of the nucleus and its possible relation to root hair elongation. Mer (53) first reported the nucleus as moving along in the hair behind its tip. Haberlandt (30) found that in many plants it lies along the outer wall of the superficial cell, near the location of the bulge which developes into the root hair. He pointed out that in wheat and *Commelina*, while the nucleus does not lie against the wall, it is connected with it by numerous plasmatic threads. He also found that the nucleus, except in *Hydrocharis*, moves into the hair after it has attained a short length, and that it remains at a rather constant distance behind the tip. This distance varies for different plants. In peas it is about 13 microns and in pumpkin about 130 microns. He concluded from his study that the nucleus is an active agent in the controlling of the growth of root hairs. More recently Haberlandt's student, Windel (87), has added evidence to support his contention. He found that in mustard root hairs, the growth is at first apical, then basal, the nucleus moving accordingly. However, Kuster (44) in 1907 published his study upon the same subject, from which he concluded that there is no relation between the position of the nucleus and the growth of the hair. He believes it to be a mere coincidence that the nucleus should in some cases lie near to the point of origin of the root hair and attaches no significance to its presence in the hair. Miss Roberts (66) confirms this view and finds great variation in the position of the nucleus in hairs which are apparently behaving alike in their development.

Ziegenspek (91) has very recently found that the root hair of *Hydrocharis* does not grow at the tip, but that the amyloid is deposited intercalarly near the base, and suggests as the explanation of Haberlandt's observations that the nucleus in this plant does not move into the hair. Besides *Hydrocharis* Kuster noted seven other genera of aquatics in which the nucleus lies always in the cell proper, and three genera in which it may lie in the middle or lower part.

By studying the same hair for a period of time under normal living conditions the writer has obtained evidence that the nucleus not only may have no active part in stimulating or controlling the growth of root hairs but apparently may even passively retard elongation, or bring about the cessation of growth. It is, for instance, found that the nucleus may enter a hair and remain there for a short time during which the hair does not grow so rapidly; and then after it retreats to the cell proper again, the hair may resume its original rate of elongation. But the more convincing evidence is obtained from a study of so-called duplex hairs, that is in cases where two hairs emerge from a common base which is formed from a bulge

of a single cell. Such instances are not uncommon on roots of collards growing in simple calcium nitrate solutions. In this case there is just one nucleus for the cell proper and for the two hairs. In some cases the nucleus may move into the base only and remain there in a central position. In such cases as have been observed the two hairs then grow at approximately the same rate. Not infrequently, however, one of the hairs assumes a more rapid growth rate before the nucleus emerges. In this instance the nucleus almost invariably passes into the hair which is growing more rapidly. It is then observed that the rate of elongation is thereupon retarded and it may even cease elongating entirely, while the rate of the other hair is accelerated. After this other hair has, perhaps, attained a greater length than the one in which the nucleus is located, the latter has been observed to move over into the hair which is now growing more rapidly (fig. 1).

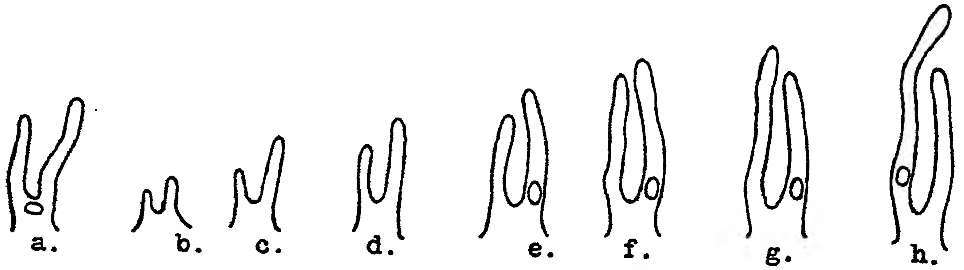


Fig. 1. Duplex Root Hairs Showing the Relation of the Position of the Nucleus to the Growth of the Two Hairs

The series *b-h* represents different stages of the same hairs

It thus seems that the growth rate is likely to determine the position of the nucleus, rather than the position of the nucleus to determine the growth rate. However the position of the nucleus does seem to have some relation to growth rate, namely to retard or stop it, rather than to accelerate or start. This relation of the position of the nucleus to the rate of growth may be explained perhaps on the basis of the relation of the nucleus to protoplasmic streaming. The protoplasm of the root hairs of many plants may be seen to be in a state of circulation, flowing from the cell proper along the inner surface of the lateral walls, accumulating in the dome-shaped tip, and then flowing back again along another wall to the cell proper. There are also commonly seen currents which cut across the interior of the cell apparently forming strands of cytoplasm which pass through the vacuoles. There may also be one or more partitions of cytoplasm which completely separate one vacuole from another. In these partitions the protoplasm streams also. Furthermore the paths of streaming may be observed to be changing rather rapidly.

It is apparent that this streaming has a direct relation to the transportation of materials dissolved in the cytoplasm. It carries, for instance, materials for growth of the root hair from the cell proper to the growing tip. This material is chiefly no doubt some form of soluble carbohydrate, such as the sugars, or soluble polysaccharids like dextrin or inulin. At the apex of the hair it is changed into the insoluble amyloid, which is deposited in the cell wall. Whether this amyloid is later transformed into the pectic bodies of the outer layer of the wall or the callose of the inner layer, has not yet been deter-

mined. But whether either or neither of these alternatives is true, it is evident that the older portions of the cell wall are composed, with one exception, of material derived only from the root proper and not ordinarily of material from the outside. There is thus need of rapid transportation in the root hair if rapid elongation is to be effected.

The one constituent of the cell wall of the hair which may be, and probably for the most part is, derived from the exterior is calcium. The fact that root hairs, as is shown below, will not grow at all without the presence of calcium in the external medium indicates that it is used directly from this source for cell wall formation. But it is hardly conceivable that the calcium could enter alone. Theoretically it is possible for it to enter by exchange with potassium or some other cation, and doubtless some potassium and perhaps magnesium is liberated from the root in this way. But there is so much calcium absorbed, and furthermore so much carbon dioxide liberated from the root, that potassium liberation is not the only thing which happens at the surface of the root hair. There must be the absorption of some anions accompanying the calcium which are not received by exchange with potassium and such ions, and to compensate for the carbon dioxide which is liberated. From a calcium nitrate solution, for instance, nitrate ions are thus absorbed. They are not used apparently in the formation of the cell wall, so that they must be conducted into the interior of the root. But nitrate ions cannot travel alone. Neither can they be accompanied by the calcium ions with which they enter, for the calcium, as we have already seen, is deposited as calcium pectate in the cell wall, or as calcium oxalate in the vacuoles. Apparently the thing that happens is that in addition to carbohydrate being transported outward in the root hair, there is also a quantity of potassium oxalate and perhaps likewise potassium pectate, which meet the calcium nitrate entering the cell and undergo exchange with it so that the calcium pectate or calcium oxalate remains in the hair and the potassium and nirate ions travel back into the cell proper. There is thus a migration of carbohydrate molecules and ions of organic potassium or magnesium salts outward and of ions of inorganic potassium or magnesium salts inward. Thus we see that the root hair is a region of considerable physical and chemical activity, and that the streaming of the protoplasm greatly facilitates these changes.

As to the effect of the presence of the nucleus in a root hair upon the streaming, it is evident that its location part way along the hair, will modify markedly the paths of streaming. It usually lies, as shown below, surrounded by cytoplasm between two vacuoles. Its size is nearly such as to completely partition the interior of the root hair. There would thus be a tendency for the material to stream out to the cytoplasm surrounding the nucleus and then be diverted back along the opposite wall to the cell proper again without passing to the dome-shaped tip at all. Thus free movement of materials from the cell proper to the tip and back may be interrupted partially or almost completely. Unfortunately in the hairs in which the nuclear migrations and cessation of growth have been observed, as noted above, streaming of cytoplasm cannot be seen, so that confirmation of this interpretation by direct observation has not as yet been made. It is thus seen that there is at least a possible explanation as to how the nucleus may operate as a passive causal agent in the retardation or cessation of growth of these root hairs.

The reason why the nucleus should move

from the cell proper into that hair of the duplex which is growing more rapidly, and should migrate from a slow growing hair to a more rapidly growing one may, perhaps, also be associated with protoplasmic streaming. The nucleus is known to move in other cells having protoplasmic movement, such as leaf cells of *Elodea* and *Vallisneria*. Whether it is carried along passively, or whether it is activated by the same principle that activates the plastids and cytoplasm is not yet known. Sokolowa, after a careful study of nuclear position and protoplasmic streaming, decided that they are interrelated. He thinks that there is an exchange between the nucleus and the stream.

Protoplasmic streaming in root hairs has been observed for many years. It is especially evident in the large root hairs of such aquatics as *Hydrocharis*, *Trianea*, and *Limnobium*. Here it is so rapid that under high magnification it takes on the appearance of the surging of the surf. Reinhardt (65) noted that upon immersing hairs to coat them with red lead, growth ceased. He also noted that protoplasmic streaming stopped. After a time both the streaming and the growth were resumed approximately simultaneously, which indicates, as suggested above, that streaming does facilitate, at least, if not condition, root hair elongation. In the small root hairs of most seedlings protoplasmic streaming is not usually apparent. Mrs. Farr (25) has reported it to be conspicuous in oats, but it is not evident in collards, rice, and similar root hairs, owing possibly to its absence, but also perhaps to the greater degree of refraction of the more highly curved surface of the smaller hairs, or to the absence of particles in the protoplasm. That protoplasmic streaming does occur in these hairs is indicated by the rather rapid change in the arrangement of the vacuoles.

The vacuolar system of root hairs has not been extensively studied. Mer first (1880) referred to them. Miss Addoms (1) describes the development of a root hair as regards its vacuoles as follows:

> In a very young root hair the protoplasm is dense and almost devoid of vacuoles. As the root hair grows, the protoplasm becomes less dense, vacuoles form and enlarge, and the cell is apparently at the height of its usefulness as an absorbing organ. The vacuoles continue to enlarge and begin to coalesce, and the protoplasm is crowded more and more toward the outside of the cell, so that finally it is but a thin film separating the cell sap from the cell wall, and the root hair is of little value to the plant.

Her interpretation of the efficiency with which root hairs function as organs of absorption, based upon the intracellular organization, is in harmony with the experimental evidence of Popesco (64), which indicates that the older hairs, that is, the longer ones, do not function in absorption.

Strugger (78) finds in barley, as does the writer (21) in collards, that the most typical arrangement of vacuoles consists in a terminal vacuole between the protoplasm surrounding the nucleus and that in the dome-shaped tip (fig. 2 (a)), and a basal vacuole, which is an extension of the vacuole of the cell proper up into the root hair to the vicinity of the nucleus. Strugger finds, however, that if the hydrogen ion concentration of the medium is increased slightly, for instance, from pH 6.6 to 6.3, the apical vacuole disappears. If it is increased still more, that is to 6.2, many small vacuoles appear. If changed to pH 6.1 secondary vacuoles disappear. A change now to slightly greater acidity, pH 6.0, gives the normal condition again. By increasing the acidity farther the cycle is repeated once, reaching a lethal acidity at pH 5.6. He finds a similar bimodal curve for streaming with a maximum rate at pH 6.15. This indicates a remarkably

high degree of sensitivity to small changes in the reaction medium. No data are given as to the percentage of root hairs in each solution in which the organization given as typical occurs. It is also to be observed that Strugger used roots which were severed from the rest of the seedling and then transferred to the solution. It has been found (12) that transfer of the root to the solution from air has a marked effect upon the development of the hairs, which varies with time after immersion. It would be surprising if severing the root from the seedling would not have even a greater effect upon the behavior of root hairs.

The writer (21) has studied in collards the vacuolar changes in root hairs which developed on the attached root some hours after immersion in solution of simple calcium salts. They were studied over a range of hydrogen ion concentration from pH 4.5 to 11.5 at one or one-half pH unit intervals. No relation between vacuolar organization and hydrogen ion concentration was detected. In each solution there was a considerable range of variation in this regard. Even in the same hair there was a change found (fig. 2 (b)) from time to time, changing visibly in the course of one or two minutes. It was furthermore found (fig. 2 (c)) that the development of an isolated vacuole in one of the hairs of a duplex may be accompanied by cessation of growth, while the other hair with a vacuole formed as an extension of that of the cell proper would continue to elongate at the normal rate. This indicates that the vacuoles may operate in much the same way as the nuclei in setting up cross currents, due to their position, which divert the main stream of materials from the tip by means of a short cut back to the cell proper, and thus bring about retardation or cessation of growth.

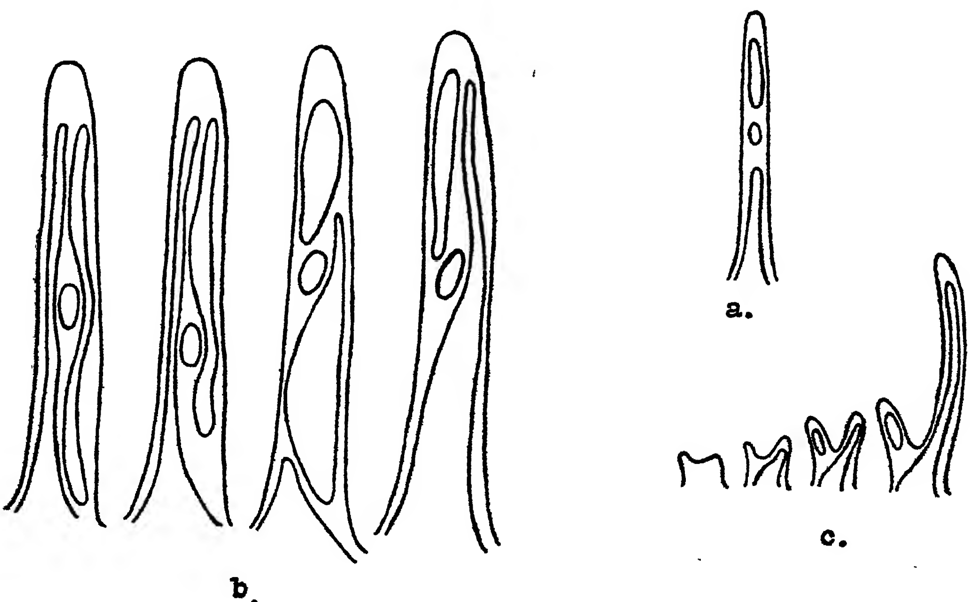


Fig. 2. Root Hairs Showing Relative Positions and Variations in Vacuoles
The series (*b*) was drawn from the same hair at intervals of a few minutes. The series (*c*) also shows the vacuolar condition during the development of a duplex hair.

Schaede (71) has studied the root hairs

of *Hydrocharis* rather intensively, using a wide variety of intravital stains. He used protoplasmic streaming as an index of the normal condition of the cell. He has been able to compare the effect of different dyes on the cell and found that most of them, with the exception of Chrysoidin, cause alterations, which he regards as injurious or lethal. He also found that the cytoplasm is basic when alive and acid when dead. Upon staining crystals appear in the hair. Whether these are precipitations due to the effect of the stain upon otherwise soluble substances, or whether they are simply making apparent otherwise invisible solids, is not clear. Martin has determined the hydrogen ion concentration of root hairs of the sunflower to be from pH 4.4 to 4.0, which is as acid as any cells of the plant and more acid than many of them.

In studying the root hairs of *Lepidium*, Zacharias (89) detected the presence of certain small bright bodies. They were found to be in Brownian movement, which was accelerated with transfer to solutions. In certain hairs no glistening bodies were present, and these hairs behaved differently to chemical tests and in their reaction to certain solutions. The writer (21) has observed the appearance of glistening bodies in hairs of collards, but only when growing in very alkaline solutions.

The osmotic pressure of the root hairs of ordinary plants has been measured by the plasmolytic method, that is, by determining the strongest solution which will not cause shrinkage of the protoplasm. Miss Roberts found that root hairs of different species were plasmolyzed by sucrase from 0.22 M to 0.4 M concentrations after growing in air, and that in solutions they maintain an osmotic pressure 4 to 6 atmospheres higher than the medium. Ursprung and Blum (81) found an osmotic pressure of 1.1 atmospheres, the lowest that they observed in any of the cells of the plant. Miss Addoms (2), however, finds that the root hairs are not plasmolyzed as readily by either salts or sugars as are other cells of the root, especially the root cap and the cortex. She finds, for instance, that 0.8 M sodium chloride or 0.5 M cane sugar will affect the latter tissues, but not the root hairs. Popesco (64) obtained similar results with plasmolysis and argued, therefore, that root hairs are not absorbing organs, whereas it simply shows that they have a higher osmotic pressure and therefore are more efficient organs for absorbing water. Ohga (58) found that the osmotic pressure of root hairs is affected by the age of the seedling and the medium. Bean, wheat, and buckwheat root hairs were plasmolyzed by 0.24 molar sucrase when the root was 5–8 cms. long and had been growing in air, but 14 days later 0.36 to 0.54 M concentration was required to plasmolyze the hairs then growing in water cultures.

Ursprung and Blum (81) found that the osmotic pressure of the root hairs depends to some extent upon the medium in which they are growing. It is 1.1 atmospheres in saturated air. Upon transfer to pure water it drops to 0.3 atmospheres in eight days. Upon transfer to 0.2 M sucrose it rises to 5.3 atmospheres in one day. The plant thus has the ability to adjust the osmotic pressure of root hairs to approximate that of the surrounding medium. It should be pointed out, however, that this adjustment is made, not by changing the osmotic pressure of a given root hair, but by sending out new root hairs in the new concentration, having a different osmotic pressure. Halophytes, that is, plants which grow in soil high in salt content, such as seaside plants, have a much higher osmotic pressure in their root hairs. Hill (34) found that *Salicornia*, for instance, will not be plasmolyzed by

5.8 per cent sodium chloride, whereas ordinary plants growing in cultivated soils cannot resist more than 1.5 per cent.

REACTIONS OF ROOT HAIRS TO EXTERNAL CONDITIONS

Root hairs are found to respond to external conditions in various ways. In the first place certain conditions will permit their development, while they will not arise at all under others. Under some conditions they burst; under others their protoplasm is coagulated. They also are found to curve in response to certain stimuli, and to change their form by varying their diameter or direction of growth. Finally they grow at different rates under different conditions.

Pfeffer (63) was the first to observe the bursting of root hairs by hypotonic solutions.

Zacharias (89) in 1891 found that the cell wall might burst and growth be continued by the formation of a new inner membrane. Klemm (39) studied the bursting and contraction of cells under various conditions, including observations on the root hairs of *Trianea*. He found that the protoplasm does not contract with high temperature, but in young hairs it does contract at low temperatures. He found that low concentrations of acids have an explosive effect on these hairs. Stiehr (77) observed bursting in root hairs of timothy when placed in 0.15 per cent to 1 per cent solutions of several common salts.

Klemm (39) observed coagulation of protoplasm of hairs of *Trianea* in 0.1 M nitric acid or oxalic acid. Miss Addoms (1) has made the most extensive study of various substances in bringing about the coagulation of the protoplasm of root hairs. She attributes it in part to high degree of acidity of the solutions, ranging as they did from pH 3.94 to pH 3.47, or to high concentration of the salts, using 0.1 M solutions of potassium, sodium, calcium, magnesium, zinc, and aluminum salts, aluminates and cyanides. She has also found that ultraviolet light may bring about the coagulation of root hairs.

The effect of light upon root hairs has been considered, especially in connection with the question of the proper conditions for their production. Schwarz found no effect (73). Constantin found that root hairs develop more in darkness than in light. Devaux (1888) found that roots in water grew faster in the dark, but that they bore few or no hairs, whereas roots in the light grew less rapidly, and bore many hairs. Later (1891) he found that in some grasses, as *Lolium*, there was a daily periodicity of root hair length in light, so that each day's production formed a cone or spindle shaped mass of root hairs. This showed that not only are more root hairs produced in light, but they attain a greater length. Went's experiments were not convincing. Pethyridge (62) on the other hand reports that light retards root hairs of wheat and oats in water cultures. Miss Snow (75) found little difference in the number or length of root hairs in light or darkness. Seidel (74) reports that only in intense light is root hair growth inhibited. Jeffs (36) made a definite study carefully measuring the elongation of root hairs in saturated air using different intensities of illumination. He found no effect of light so long as temperature is kept constant. It thus seems that much of the earlier work indicating a definite effect of light on root hair production and growth is not supported by more recent and more detailed observations.

The first definite study of the effect of temperature on root hair production was made by Miss Snow (75). She found that wheat produces numerous hairs between 4.5° and 11.5°C., fewer between 16.0° and

29.5°C., and none at higher temperatures. Corn likewise produces none above 27.0°C. Jeffs (36) studied the effect of varying the temperature upon the rate of elongation of a single hair. He found that a very slight change, two or three degrees, in either direction caused either a temporary or a permanent cessation of growth. In many cases where growth was resumed, there was apparent an enlargement of the root hair during the period of adjustment to the new temperature. Schwarz (73), Pfeffer (63), Went (85), and Miss Snow all agree that contact in itself is not a factor in root hair production, but that the effect is a chemical one.

The most extensive study of root hair production has been upon the effect of water and air respectively. Martin found them shortest in water, longer in soil and longest in air. Mer (53), who was one of the first to consider this question, attributed the lack of root hairs on many species in water to the stimulating effect of the medium upon root elongation. He found that roots in air have root hairs developing much nearer the tip than those in water; that is, the region of elongation of the root is greater in water. He concluded therefore that the production of root hairs was a response to inhibition of root elongation. He also pointed out an inverse relation between root-hair production and production of lateral roots which was later confirmed by Constantin (4) and Lesage (48). Miss Snow found that corn, which normally does not produce root hairs in an aqueous medium, may be induced to do so by increasing the oxygen supply of the water in which it is grown. Vöchting (83) found that a reduction of the O_2 content of the air to 3 per cent inhibited the production of root hairs in water. Surprisingly few species of plants have been reported as producing root hairs in water. The writer has compiled (12) a list from the literature, and added several, making a total of only 87 species. It is not considered, however, that this list is by any means complete. Many plants, which have been reported as not producing root hairs in water, will undoubtedly be found to do so, when the proper adjustment is made of oxygen content, hydrogen ion concentration, osmotic pressure, and chemical composition of the solution. Mer (54) found that even onion roots will produce root hairs if left in air long enough.

Not much evidence has been accumulated as to the effect of highly concentrated solutions, that is solutions of high osmotic pressure of the medium, upon root hair production. Patschovsky (60) found that rhizoids of *Chara* are inhibited by an 8 per cent Knop's solution, whereas they grow well in a 1 per cent solution. The writer (13–24) has studied the rate of elongation of root hairs of collards in different concentrations of calcium chloride and calcium nitrate. He found that above the optimum concentration, about 0.020 molar solution, the rate falls off at first rapidly with increased concentration, and then more gradually, reaching a maximum concentration in the case of chloride at about 0.185 molar solution. If, instead of adding additional salt to the optimum concentration, which is about equivalent in osmotic pressure to a 1 per cent Knop's solution, sugar be added, it is found that a similar drop in rate of growth occurs to that which is obtained by adding equimolar amounts of the salt. It is therefore concluded that above a certain concentration osmotic pressure of the solution does have a retardative effect upon root hair elongation.

Krassnow (42) and Gerneck (27) both found that roots were much more abundantly haired in $Ca(NO_3)_2$ than in KNO_3.

Micheels (57a) found root hair elongation more rapid in nitrate than in chloride. Hansteen (31), Coupin (5), Kuster (44), Trelease (79), and the writer (14), all find that calcium is apparently necessary for root hair production. Hansteen has been the most ardent and insistent advocate of this view in repeated papers (31, 32). Kisser (38) has, however, demonstrated it in the most convincing manner. He supported seedlings in a chamber in such a way that no contact of the seedling was made with substances containing calcium. For this purpose he found it necessary to use special calcium-free cloth and glass. In this case the root grew, but no root hairs were formed. If, however, the slightest trace of calcium came in contact with the root, root hairs emerged. Hansteen (31) found that the calcium must be absorbed from the exterior in order for root hairs to appear. He grew seedlings with one root in a calcium solution and the other in a solution of some other salt, and found root hairs only on the former. Only one reference (49) is found in the literature to root hairs developing in solutions of single salts other than those of calcium, and in this case it is not unlikely that impurities may have been present. Both Kisser and Hansteen found that magnesium, potassium, and pure water suppress development of root hairs. The writer has confirmed these findings for pure water. The significant feature with regard to calcium in relation to root hairs seems to be that it is utilized directly in cell wall formation, and is in fact, the only constituent of the cell wall which is not synthesized within the plant.

Sachs (67) was the first to attempt an explanation of the curving of root hairs around soil particles. He attributed it to thigmotropism, that is, a response to contact with soil particles. Schwarz (73) concurred in this interpretation and noted that such curvatures do not occur in water or in saturated air, where no solid bodies come in contact with root hairs. Jost and Pfeffer, the leading plant physiologists of the last part of the last century, accepted this interpretation also. No further studies were, however, made until very recently, when by a careful and thorough investigation Kurt Seidel (74) found that this interpretation is incorrect, and that the curving of root hairs in soil is a chemotropism, and not a thigmotropism.

Seidel noted that root hairs of lamb's quarters, *Chenopodium*, curve toward cast-off pieces of the root cap of the same plant. He then used various parts of this and other plants, fresh and decomposed, also various organic and inorganic compounds, and finally purified quartz crystals alone. He found no response at all to the latter. He did find that *Chenopodium* gives a positive curvature toward all soluble phosphates, while salts of other simple cations, sodium, iron, potassium, calcium, magnesium, ammonium, etc., gave no effect. Neither oxygen nor carbon dioxide brings it about; neither does acidity or alkalinity. The minimum threshold concentration for potassium acid phosphate is 0.0025 to 0.0040 per cent. The maximum was about 2 per cent, in which case 33 per cent of the hairs reacted, and the others appeared injured. Seidel demonstrated by a number of ingenious experiments that the normal direction of root hairs at right angles to the root is not a matter of mutual repulsion or attraction. When he fitted a glass sleeve over the root, for instance, the hairs grew out normally above and below it without curving. He also observed that the root hairs on the concave side of a curved root are straight and cross each other, showing no mutual interaction.

With regard to other species, he found

that *Rheum*, *Brassica*, *Lepidium*, and *Plantago* are like *Chenopodium* in being positively chemotropic to phosphates. Oats, wheat, barley, and millet react, however, to ammonium compounds instead of phosphates. *Agrostemma*, another grass, reacts, on the other hand, only to nitrates. *Lychnis cornonaria* and *Oenothera*, the evening primrose, react both to nitrates and phosphates. *Ornithopus* reacts to phosphates and to all potassium compounds. No instance was found of a negative chemotropism, that is, a curvature away from a substance. All of the plants named above react also to soil particles; but root hairs of *Urtica* (a nettle), *Nicotiana* (tobacco), and *Verbascum* (mullein) react neither to soil particles nor to salts. He concluded that the region of sensitivity and the region of activity were both located in the tip of the root hairs. He found no correlation between the specific reaction of the plant to these substances and its momentary need of them. There thus seems to be no possibility of a teleological explanation of these reactions. It is apparent, however, that they tend to lead the root hair in its growth in the soil in the direction of increasing concentrations of nutrients, and to become appressed to soil particles, along which these solutions migrate, and from which their content is replenished by action of root hair secretions and by bacterial processes.

THE RATE OF ELONGATION OF ROOT HAIRS

It is rather surprising that with all the study of root hairs in almost every other possible aspect no attention has been paid until now to the rate of elongation. The only reference in the literature, prior to the work of the writer is that of Reinhardt in 1892 (65), who determined the increase in length of root hairs of *Lepidium* during a period of 24 hours, and records his results by a simple statement that they grow from 0.3 to 0.7 micron per minute, and may attain a rate of 0.9 micron. Sokolowa (fig. 3) drew the form of the tip at 1 minute intervals for 12 minutes and thus showed that the tip does not grow symmetrically but that the area of enlargement shifts from side to side slightly. The writer has found, by measurement, that while the rate is fairly constant over hourly periods, it varies considerably for ten minute intervals. The writer first measured (11) the rate of elongation of root hairs produced on cuttings of *Tradescantia fluminensis* growing in Knop's

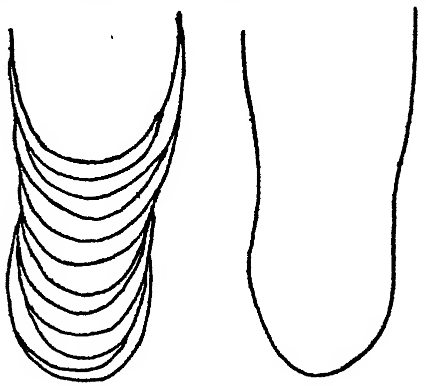


Fig. 3. (*a*) Sketches made of the tip of a root hair of *Brassica napus* at successive one-minute intervals, showing the form changes and shifting of the area of cell wall extension during growth. (After Sokolowa.) (*b*) Sketch of the form of the root tip resulting. (After Sokolowa.)

solution and in tap water respectively. Readings were taken at ten minute, or in some cases at longer intervals, over a period of several hours. It was found that the rate of elongation was more rapid in tap water than in Knop's solution. Because of the variability of tap water, and the complexity of the nutrient solution, these results were not of great significance.

Seedlings have, however, proved more suitable for such studies, inasmuch as they can be grown in small chambers on the stage of the horizontal microscope.

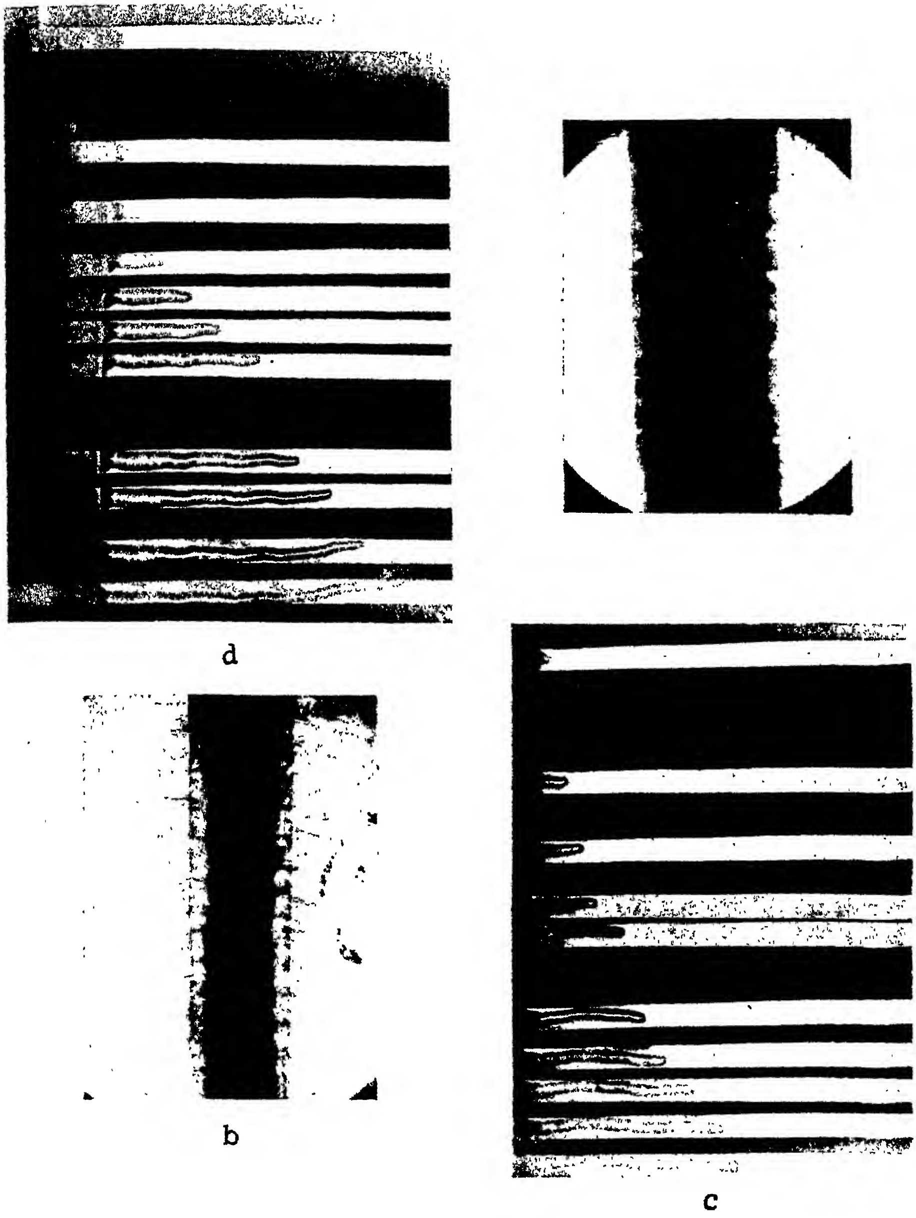


FIG. 4. (*a*) Photograph of the radish root in the root hair zone. (*b*) Photograph of the popcorn root in the root hair zone. (*c*) Root hair of popcorn photographed at 15-minute intervals. Spaces between the upper five photographs show lateral movement. The lower five show root hair elongation only. (*d*) Root hair of radish photographed at 15-minute intervals for 2½ hours. The spaces between the upper seven photographs show the amount of lateral movement during each interval. The lower four show root hair elongation only. (After Jeffs.)

Jeffs (36), working under the writer's direction, was the first to study these, using corn, radish, and mustard in saturated atmosphere. He determined first the grand period of growth of these hairs, taking readings at fifteen minute intervals for periods up to ten hours. He found that the grand period extends, under these conditions, for from ten to fifteen hours. The curve is of the typical sigmoid form with an acceleration during the first two hours, and finally a retardation, during two or three hours.

In the case of root hair growth, however, there seems to be a definite explanation of the acceleration during the first part of the grand period of growth, which is peculiar to the root hair situation. It is to be observed that this period of acceleration does not occur in root hairs growing in aqueous media (11, 14, 15, 16, 17). In water root hairs elongate at a constant rate from the start. It has been noted above that root hairs in air occur much nearer the tip of the root than they do in water; and Jeffs (fig. 4) found that this involved an overlapping of the region of root hairs with the region of root elongation. That is, the root hairs which are just emerging in air, are on the upper portion of the region of root elongation. This is shown by the fact that these very young root hairs are carried along downward very slowly during the first two or three hours of their development. The rate at which they are thus carried along, which is referred to as their lateral movement, becomes less and less during this period, so that at the close of the interval they cease this movement. It is observed that this retardative lateral movement is coincident with the acceleration of their elongation. It is thus apparent that as the epidermal cell decreases its rate of elongation vertically, it increases its rate of elongation horizontally, that is the elongation of its root hair. Thus it appears that cell enlargement may proceed during this process at a rather constant rate. The absence of such a period of acceleration of root hair elongation for roots in water simply means that the cells of the root have already ceased vertical elongation in the region which is producing root hairs. The graph for the grand period of growth for root hairs in water is then not the typical sigmoid form, but consists of a rather straight line with, in some cases, a retardation to zero near the end of the period.

An intensive study has been undertaken by the writer (14) of just one variety, Georgia collards, of just one species of plant, *Brassica oleracea*. To this same species belong cabbage, cauliflower, kohlrabi, Brussels sprouts, etc. Seedlings are chosen as nearly as possible of the same age, and placed in a chamber on the stage of the horizontal microscope, in such a position that the root is immersed in a solution, while the shoots develop in the air. The solution in the chamber is kept flowing at a rather constant rate, so that during the period of the experiment, which is 16 hours, there is practically no change in the chemical composition of the solution. The solutions thus far used have been of single calcium compounds, namely, the hydroxide, chloride, and nitrate. The experiments were performed in duplicate for each molar and hydrogen ion concentration. Previous to insertion of the seedlings a solution of known molar concentration and known degree of acidity or alkalinity was aerated with carbon-dioxide-free air, so that it contained an abundant supply of oxygen, but little or no carbon dioxide. The entire experiment was performed in a dark room of reasonably constant temperature. The only illumination consisted of a very weak red light which was used during the period

of taking observations, namely, between 12 and 16 hours after insertion.

Measurements of the length of 8 to 16 root hairs on each root were made at ten minute intervals during three hours beginning 13 hours after insertion of the root in the solution. The root hairs measured were such as appeared after ten hours immersion, that is, after the root had become entirely adjusted to the solution.

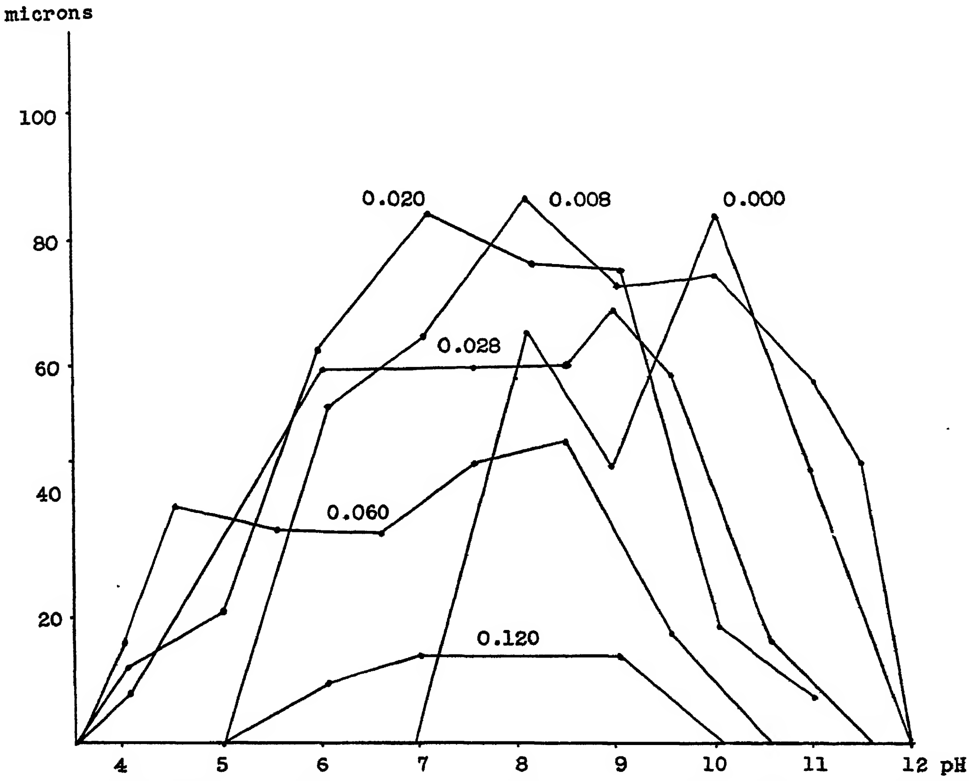


FIG. 5. GRAPHS REPRESENTING THE RATE OF ROOT HAIR ELONGATION OF COLLARDS IN SOLUTIONS OF DIFFERENT MOLAR CONCENTRATIONS OF CALCIUM CHLORID, PLOTTED ALONG THE SCALE OF HYDROGEN ION CONCENTRATIONS. THE GRAPH LABELED 0.000 IS FOR CALCIUM HYDROXIDE

The determination of the rate of elongation of root hairs in calcium hydroxide is of interest because it is the simplest solution in which they will grow at all. It is highly interesting, therefore, to find that in this simplest solution they have been found to grow faster than in any other medium so far studied. It was definitely shown (14) that they will not elongate in distilled water during the period studied. In fact few root hairs are produced after immersion in pure water. Inasmuch as the different molar concentrations of calcium hydroxide differ in the degrees of their alkalinity, the constitution of these solutions may be determined either volumetrically or colorimetrically. Both methods were employed. The initial study with calcium hydroxide was made in 1926 (14), and the study was repeated the next year (20), completely confirming the previous results.

It was found that the rate of elongation rises from zero at pH 7 (fig. 5), neutrality, to a first optimum at pH 8, and then drops to a median minimum at pH 9.0, rising to

a second optimum at pH 10.0 and then at higher concentrations dropping to zero at pH 12.0. The rate at pH 10.0 is the most rapid, being an average of 97.0 microns per hour for all root hairs measured, and in the case of one hair attaining a rate of 114.2 microns per hour, which was the most rapid growth obtained for any hair of the 3500 or more so far measured in this and other solutions.

It is perhaps significant to observe that the simplest solution in which root hairs will grow supports the most rapid growth. While other solutions may be found later which will give still more rapid elongation, yet this indicates the [illegible]at importance of calcium to root ha[illegible]gation, and perhaps the lack [illegible]y that any other mineral e[illegible]nt be [illegible]ent on the outside. That calcium is utilized directly in root hair elongation is indicated by the fact that it is not the lowest concentration of calcium hydroxide that supports the most rapid growth. It is apparently the highest concentration which can overbalance the inhibitory effect of the hydroxyl ion. This is further indicated by a comparison of root and root hair elongation in calcium hydroxide. Root elongation rises to an optimum at pH 8.0 or 8.5, above which it drops off gradually to zero without rising to a second optimum. This indicates that at least in these dilute solutions the calcium does not penetrate into the interior of the root, but is consumed largely or entirely by the superficial cells, especially the root hairs; while the hydroxyl ions do penetrate and in the more alkaline solutions have a retardative effect upon root elongation.

The bimodal graph for variations in hydrogen ion concentration has been secured for a large number of biological reactions, especially those involving growth. Salter and McIlvaine obtained it for the growth of wheat seedlings, Hixon for the germination and growth of seedlings of various plants, Olsen for the growth of plants to maturity, Hopkins for the development of a fungus, *Gibberella*, Cole for the growth of roots of corn seedlings, Arrhenius for the extension of leaf areas and growth of plants in water, sand, and soil, Cohen and Clark for the number of viable bacteria of *Bacillus dysenterica*, Robbins for the growth of fungi and reactions of potato tubers, McSwiney and Newton for reactions of smooth muscles, Herčík for root growth of *Pharbitis*, and Hopkins for locomotion of *Amoeba*. Similar bimodal curves have been obtained with non-living colloids, with regard to their swellability, precipitation, viscosity and other properties. Loeb demonstrated that in the case of certain proteins the median minimum of [illegible]ese curves was located at the hydrogen ion concentration of the isoelectric point of the protein. It has therefore been concluded by Robbins and others that the depression in the pH graph for growth was indicative of and a response to the isoelectric point of the constituent proteins. Pearsall has found in some cases trimodal and multi-modal graphs for the response of plants to changes in pH, and suggests that the various depressions in the graphs indicate the respective isoelectric points of the constituent proteins.

It is obvious that a much more extensive study is necessary in order to ascertain the growth rate of root hairs in different solutions of other calcium compounds than the hydroxide. With the hydroxide, hydrogen ion concentration is proportional to molar concentration, and hence there are only two variables, concentration and rate of elongation. With simple calcium salts, however, the hydrogen ion concentration may vary without changing the molar concentration, and vice versa, so that there are three variables:

hydrogen ion concentration, molar concentration, and rate of elongation.

The lowest molar concentration of calcium choride (16) studied thoroughly was 0.008. It gave a pH range from 5.9 of 0.028 M had a range of 3.9 to 10.4, with optima at 6.5 and 9.0, the alkaline optimum in this case being the greater, while at lower concentration of the salt it was the lesser. In 0.060 M the range is

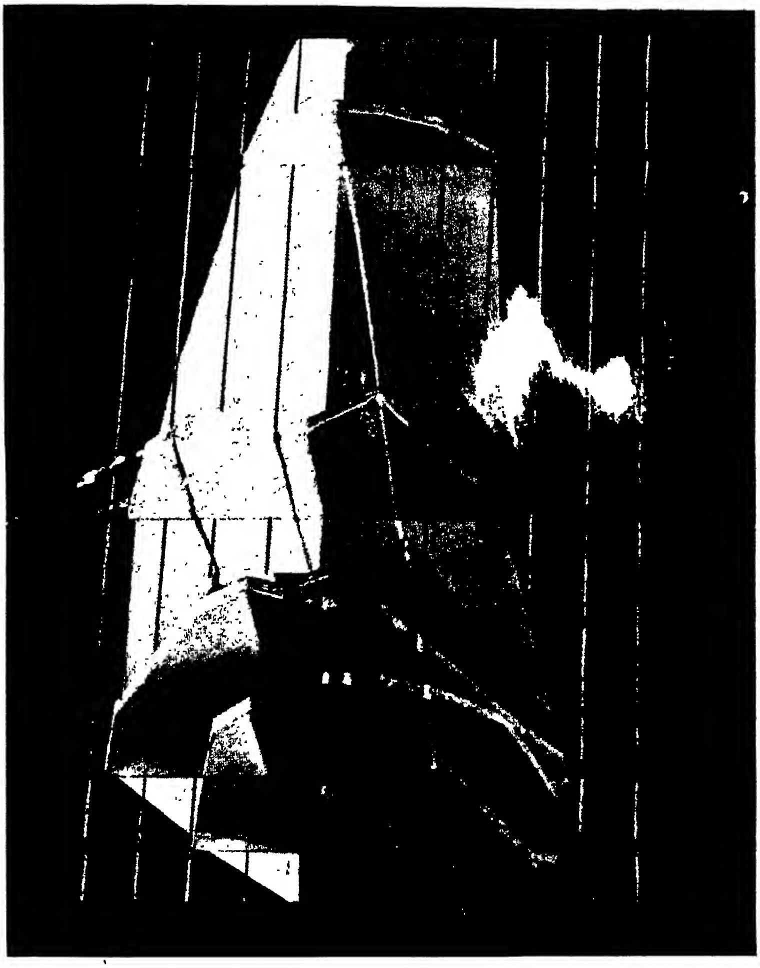


FIG. 6. A MODEL SHOWING GRAPHS SIMILAR TO THOSE GIVEN IN FIGURE 5 DISPOSED UPON A PLANE AT DISTANCES COÖRDINATE WITH THE MOLAR CONCENTRATIONS

The graphs here used are based upon the most rapid root hair measured, rather than on the average. The result is not substantially different, except that no median minimum is apparent in 0.008. This model shows that the optima and the median minima fall in approximately straight lines.

to 11.4 with a distinct optimum at pH 8.0 and a lower and less distinct optimum at 10.0 (fig. 5). A concentration of 0.020 molar gave a range of 3.4 to 11.4 with optima at 7.0 and 9.0. A solution 3.5 to 9.5, with the lesser optimum at 4.5 and the greater at 8.5. In 0.120 M calcium chloride the range is 6.0 to 9.0 with just one optimum at 7.0.

It is apparent that these data can be

better correlated if they be plotted in three dimensions. A model was therefore constructed (fig. 6) representing the rate of elongation plotted against pH by erect cards, standing on a platform, the two dimensions of which are spaced to correspond to the hydrogen ion concentration and the molar concentrations respectively. It is found by this arrangement that the alkaline limit falls in a straight line, and that the acid limit forms a curve at low concentrations and at higher concentrations forms a straight line intersecting the alkaline limit at neutrality and a molar concentration of theoretically 0.185. This relationship can better be shown by a map or floor-plan of the model (fig. 7). In this also it is shown that the alkaline optimum and the acid optimum form straight lines, with the median minimum between. It need scarcely be pointed out that it is necessary to incorporate the graph for calcium hydroxide in these models and maps inasmuch as it may be looked upon as representing zero concentration of the salt.

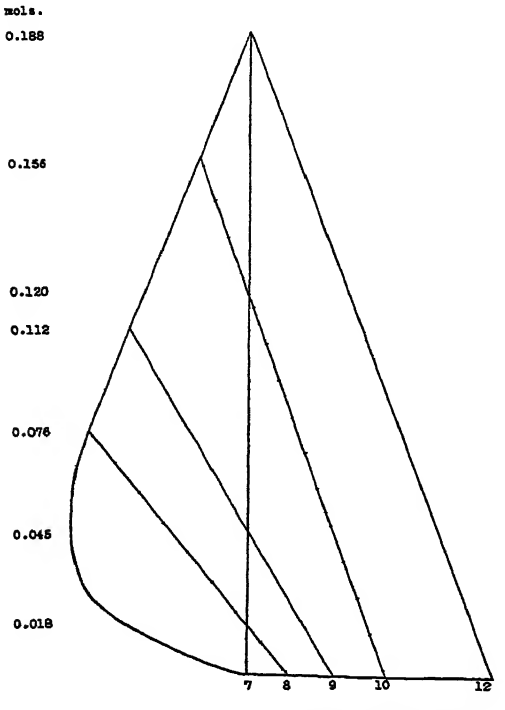


FIG. 7. IDEALIZED FLOOR-PLAN OF TRI-DIMENSIONAL GRAPH FOR $CaCl_2$. DOTTED LINES INDICATE MAXIMA

From this model and map there can be readily pointed out the relationship between the effect of the respective ions present namely, Ca, Cl, H, and OH, and their mutual interaction. For instance, it is seen that no growth occurs in acid solutions of low calcium content. This is in harmony with the agricultural experience of the inadequacy of acid soils low in calcium, and indicates a possible explanation of the beneficial effect of adding calcium to an acid soil, if by so doing the root hair elongation is changed from zero to the maximum rate in any concentration of this salt, namely at a concentration of about 0.010 and neutral or slightly alkaline solutions. The growth of root hairs in acid solutions, with moderate calcium present, indicates that the latter ion has an antagonistic effect upon the hydrogen ion. This is also in harmony with the results of others upon studies in plant development. At still higher concentrations of the calcium, however, a new relationship is brought out, namely that the hydrogen ion does not have an antagonistic effect upon the calcium ion, that is, in higher concentrations of calcium chloride no growth occurs in very acid solutions. In like manner relationships may be pointed out between the chlorine ion and the hydroxyl ion on the alkaline side. The interpretation here is however complicated by the difference of interpretation of alkalinity as due either to the presence of the OH ion in excess or simply to the decrease in amount of free hydrogen ion. It is also complicated by the fact that the calcium seems to play a direct part in the growth of the root hair, and

the rôle of the chlorine is thus probably secondary. The effect of the anion upon root hair elongation can thus better be ascertained by a comparison of the one anion with another, such as chloride with nitrate. This will be done below.

The results for the growth of collards in calcium nitrate are given in the accompanying figures (8 and 9). It is apparent that at low concentrations the pH graph however, some differences. The maximum rate is slightly less in nitrate than in chloride. The range does not extend quite so far on the acid side in nitrate; but it is apparent that the antagonism of calcium for hydrogen ions is greater in the nitrate than in the chloride. That is, the addition of less nitrate to an acid solution is necessary in order to permit it to produce root hairs, than of chloride.

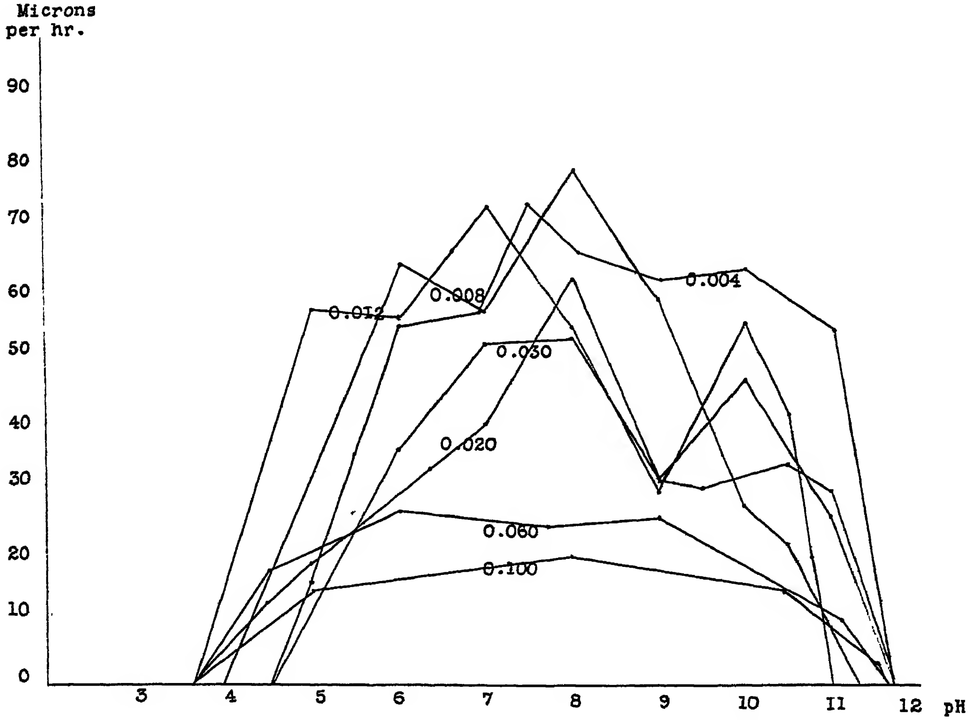


Fig. 8. Average Rate of Root Hair Elongation in Calcium Nitrate

for nitrate is trimodal, for medium concentrations it is bimodal, and for high concentrations it is monomodal. The relationship becomes, however, perfectly clear when we consider the data in terms of the three dimensions.

The results for nitrate approach very closely to those for chloride (fig. 10) and indicate that the cations have doubtless much greater effect upon root hair elongation than do the anions. There are, By the construction of similar maps to these for each of the nutrient and non-nutrient anions it is hoped that a clear picture may be presented of the effect of each constituent of the nutrient and then of the soil solution.

It is important to notice the very wide range of hydrogen ion concentration in which the root will produce root hairs. This is not to be taken as an indication of the ability of root hairs to adjust them-

selves to a wide range of conditions. On the contrary, they are extremely sensitive to changes in the medium, as was pointed out above in regard to temperature, and as will be shown below. But it does show clearly that the root has a great ability to adjust itself to a wide range of conditions, and to produce root hairs in solutions of many different constitutions. The prime requisites seem to be that calcium be present, and that the minimum amount of calcium supplied be greater the greater the acidity of the solution, that the solution shall not be too strongly alkaline or acid, and that the concentration of the salt must not be too high since the resistance to acid and alkali is less at high concentrations.

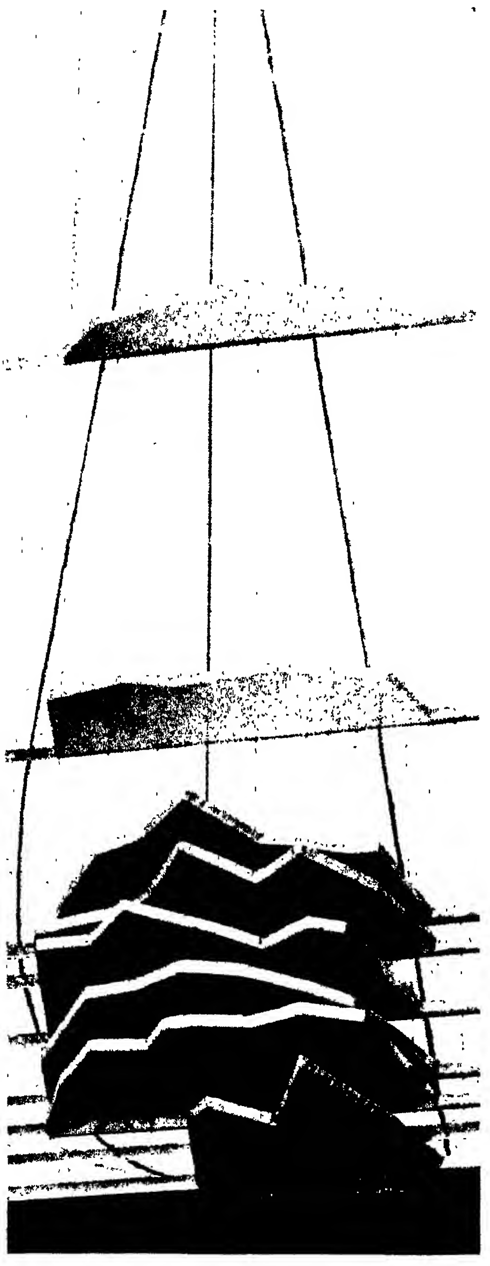


Fig. 9. Tri-dimensional Graph Showing the Rate of Growth of Root Hairs of Collards in Concentrations Ranging from 0.004 M to 0.100 M and in Different Degrees of Alkalinity and Acidity

It is to be observed that the data referred to above on the rate of elongation of root hairs in different solutions were obtained from hairs which appeared on the root ten or more hours after immersion in the solution. A consideration of the growth rate of root hairs which had been growing in air might yield somewhat different results. A limited study was made to ascertain the rate of elongation of these so-called amphibious root hairs several hours after immersion. It was found that only in solutions which support the optimum growth rate did they continue to grow during the first two hours after immersion. In all other solutions they did not grow during the first two or three hours, and then they began growing at a rate coördinate with that obtained for the aquatic hairs in the same solution. However, in especially concentrated solutions the older root hairs collapsed, those a little younger ceased growing, but did not change their form, those still younger grew after a period of rest, but changed their form or direction, while the youngest resumed growth apparently normally.

This method of studying the rate of elongation of root hairs and of plotting tri-dimensional graphs affords a means

not only of comparing one ion with another, one calcium compound with another, and one more complete solution with another, but also of comparing one kind of plant with another. Mrs. Wanda K. Farr has already begun this work. She finds that rice, with respect to its root hair elongation, exhibits a greater tolerance for acid and less tolerance for alkali than do oats or collards. The acid limit for rice was found to be pH 2.5.

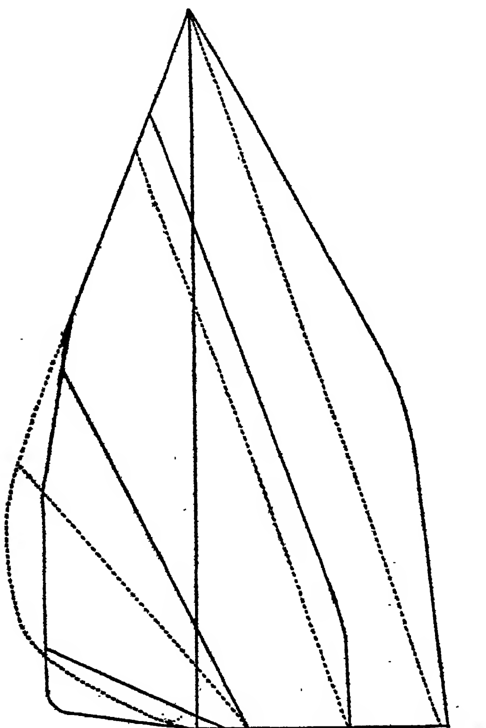


FIG. 10. CALCIUM NITRATE MAP ——— SUPERIMPOSED UPON THE CALCIUM CHLORID MAP -------

ABNORMAL FORMS OF ROOT HAIRS

The typical form for the root hairs of many plants in air and in aqueous media is cylindrical, straight, at right angles to the root, with dome-shaped tip. The root hairs of these same plants, however, growing in soil, take on many different forms, as Sachs (67) described and figured for wheat, oats, clover, and *Selaginella*. This is doubtless a response to contact with the soil particles, and to reactions to the chemicals present in the soil solution. The hairs under these conditions become enlarged at the tip, crooked, knotty, and branched. The writer (12) has found that some plants, as buckwheat, amaranth, millet, *Saponaria*, and *Gysophila*, produce root hairs which are bent, curved, or crinkled, even in aqueous media.

A number of investigators have accumulated observations as to the effect of external conditions in bringing about changes in the form of otherwise typically cylindrical hairs. Persecke was among the first to describe the various forms of root hairs. Schwarze noted a large number of peculiar forms assumed by root hairs of various plants in the presence of soil particles, in various solutions, and upon transfer to various liquid media. Wortmann (88) observed some of these forms of root hairs in sugar or potassium nitrate solutions. Reinhardt (65) noted the swelling of root hairs in these solutions and the resumption of normal form later. Sokolowa (76) has studied it very extensively, attempting to correlate the changes in form with nuclear position, lines of flow of protoplasm, oxygen content of the medium, etc. Stiehr (77) produced a number of abnormal forms of root hairs with organic compounds, such as sugars and alcohols, and with the electric current. Reference has already been made to the observation of Jeffs (36) as to the swelling of the hair in response to changes in temperature. The writer has studied the effect of calcium chloride and calcium nitrate of different hydrogen ion and molar concentrations upon the forms of aquatic and amphibious root hairs.

It has already been pointed out that very old root hairs which persist on roots have been found by McDougall (52) to have a greater diameter, with brown and thickened walls. Watson (84) has noted that on old roots of the sunflower the root hairs may branch.

A special type of abnormality of root hair growth is the so-called cap formation. It was first observed by Wortmann (88), and was later studied by Zacharias (89), Reinhardt (65), and Stiehr (77). It consists in the formation of a new wall a short distance from the tip, cutting off a short portion. In some cases Reinhardt showed several such partitions. It is usually followed by the formation of a side branch just behind the cap, which may grow out at right angles, or curve, or later resume a direction parallel to the original hair. Zacharias (89) attributed it to the plasmolysis of the protoplasm by the changed environment, while Reinhardt attributed it to cessation of growth, and resumption in a new direction. He correlated it with peculiar type of growth by Krabbe in bast cells.

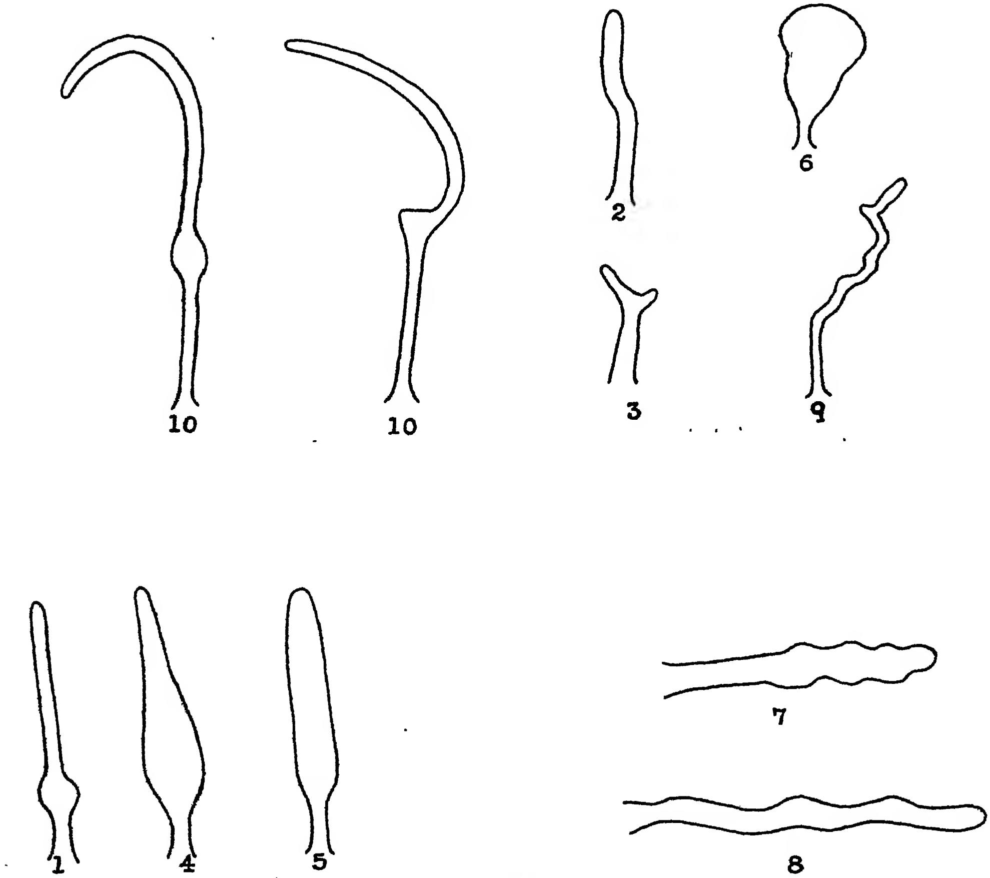


FIG. 11. TYPES OF ABNORMALITIES IN ROOT HAIRS

Stiehr (77) found a variety of changes in form upon the change of the concentration or the composition of the medium. The writer has found that these changes occur when the root is transferred from satu-

rated air to a solution, and less frequently in root hairs newly formed in the solution.

Wortmann (88) attributed these changes to alterations in turgor pressure. Sokolowa (76) considered that they are due to alterations in the oxygen pressure of the medium. It is not unlikely that more than one condition in the environment may bring them about.

The writer (fig. 11) has attempted to classify these changes in form under two types, namely changes in extent of the growing area at the tip of the hair, and changes in the direction of growth. The simplest type of modification is the so-called swollen (fig. 11 (1)), in which there is a temporary change in diameter and a later resumption of the same diameter. This type appears to be the most common in solutions of low toxicity, and is the one found by Jeffs for temperature changes. The next type is the kinked, in which there is a temporary change in direction with a subsequent resumption of growth in the original direction (fig. 11 (2)). These two types may be taken as showing a minimum of injury due to the changed environment. The next is branching. This consists in an increase in the extent of the growing area followed by a restriction again, as in the swollen, but now with two loci instead of one. This necessarily involves a permanent change in direction of at least one of the branches and usually of both and is not to be confused with the duplex hairs discussed above. Van Tieghem (82) noted such double hairs in three species of *Distichia*. Haberlandt (29) reported it about the same time, 1887, in *Brassica napus* and other cruciferae. Hill reported it in hairs growing in concentrated solutions (34), and Miss Roberts (66) figured it. The writer (19) has noted it in calcium chloride, but more commonly in calcium nitrate, where it is found in amphibious hairs and also in the aquatic hairs developing after immersion in the solution.

The flask-shaped hair (fig. 11 (4)), is not so common, but is an example of response to the shock of immersion by enlarging the areas of growth, and then a gradual recovery to normal diameter and direction. The inflated hair is by far the most common in very toxic solutions, and in the most toxic solutions which will support growth at all it is the only type found. It consists in (fig. 11 (5)) increase in diameter and continued growth at this new diameter. Hence there is no recovery to the original type. The most extreme type of abnormality, as judged on this basis, is the spatulate. It consists of growth at a progressively greater and greater diameter (fig. 11 (6)).

Next to the types of abnormalities which involve a modification followed by a return permanently to the normal, there are types of modification which display a periodicity between the new and the old. Such is for instance the beaded, in which there is an enlargement followed by (fig. 11 (7)) a return to the original diameter, then an enlargement, then a return, etc. These were not found in calcium chloride, but were not uncommon in calcium nitrate of a high pH, namely 11.0. A corresponding type, but consisting of an alteration of direction, instead of diameter, is the undulating (fig. 11 (8)), which was very much more frequent.

Perhaps the most extreme type of all is the so-called crooked, (fig. 11 (9)) in which there is a progressive enlargement or diminution of diameter, and change of direction, without any apparent rule.

The curved (fig 11 (10)) is a type in which there is a progressive change of direction.

This classification of the abnormalities of root hair form indicates that root hairs

undergo all degrees of shock and recovery. There is the temporary change with complete recovery; there is the temporary change with temporary recovery, followed by a recurrence of the new feature. There is the temporary change with a slow recovery; there is the change with slight permanent effect; there is the change with marked permanent effect. There is the change which becomes progressively more and more removed from the original type, and finally there is a complete upset of balance. Such is the response which root hairs give to changed environment; it is also the response which all living things are likely to give in a greater or less degree to sudden alteration of their surroundings, and even serves to indicate that the responses obtained in human beings to extreme conditions such as shell-shock, etc., are merely expressions of a fundamental property of protoplasm.

LIST OF LITERATURE

(1) Addoms, Ruth M. 1923. The effect of the hydrogen ion on the protoplasm of the root hairs of wheat. Amer. Jour. Bot., 10: 211–220.

(2) ———. 1927. Toxicity as evidenced by changes in the protoplasmic structure of root hairs of wheat. Amer. Jour. Bot., 14: 147–165.

(3) Bardell, E. 1915. The production of root hairs in water. Univ. Washington Publ. Botany, 1: 1–19.

(4) Costantin, M. J. 1885. Recherches sur l'influence qu'exerce le milieu sur la structure des racines. Ann. d. Sci. Nat., VII, 1: 135–182.

(5) Coupin, H. 1917. Influence des sels de calcium sur les poils absorbants des racines. Compt. Rend. Acad. Sci. Paris, 164: 641–643.

(6) ———. 1919. Sur le pouvoir absorbant du sommet des racines. Compt. Rend. Acad. Sci. Paris, 168: 519–522.

(7) Cowles, H. C. 1911. Ecology. Vol. 2, A Textbook of Botany, Coulter, Barnes and Cowles. American Book Co., N. Y.

(8) Devaux, H. 1888. De l'action de la lumière sur les racines croissant dans l'eau. Bul. Soc. Bot. France, 35: 305–308.

(9) ———. 1891. Croissance des poils radicaux. Bul. Soc. Bot. France, 38: 51–52.

(10) Farr, C. H. 1924. Cellular interaction between host and parasite. Phytopathology, 14: 575–579.

(11) ———. 1925. Root hair elongation in Knop's solution and in tap water. Amer. Jour. Bot., 12: 372–383

(12) ———. 1925. The formation of root hairs in water. Proc. Iowa Acad. Sci., 32: 157–165.

(13) ———. 1927. The isoelectric point and the median minimum of growth. Proc. Soc. Exper. Biol. and Med., 24: 715–716.

(14) Farr, C. H. 1927. Studies on the growth of root hairs in solutions. I. The problem, previous work, and procedure. Amer. Jour. Bot., 14: 446–456.

(15) ———. 1927. *Ibid.* II. The effect of concentrations of calcium nitrate. Amer. Jour. Bot., 14: 497–515.

(16) ———. 1927. *Ibid.* III. The effects of concentrations of $CaCl_2$ and $Ca(OH)_2$. Amer. Jour. Bot., 14: 553–564.

(17) ———. 1928. *Ibid.* IV. The pH-molar-rate relation for calcium chloride. Amer. Jour. Bot., 15: 6–31.

(18) ———. 1928. *Ibid.* V. Root hair elongation as an index of root development. Amer. Jour. Bot., 15: 103–113.

(19) ———. 1928. *Ibid.* VI. Structural responses to toxic pH and molar concentrations of $CaCl_2$. Amer. Jour. Bot., 15: 171–178.

(20) ———. 1928. *Ibid.* VII. Further investigations upon collards in calcium hydroxide. Bull. Torrey Bot. Club. In press.

(21) ———. 1928. *Ibid.* VIII. Structural and intracellular features of collards in calcium nitrate. Bul. Torrey Bot. Club. In press.

(22) ———. 1928. *Ibid.* IX. The pH-molar-rate relation for collards in calcium nitrate. Ann. Mo. Bot. Garden. In press.

(23) ———. 1928. The effect of Ca and H ions upon root hair growth. Proc. First Intern. Congress Soil Science, 1927. In press.

(24) ———. 1927. The elongation of root hairs in solutions of single calcium compounds. A comparison of three anions: nitrate, chloride, and hydroxide. (abstracts only) Amer. Jour. Bot., 14: 627.

(25) Farr, Wanda K. 1927. The elongation of root hairs in solutions of single calcium com-

pounds. A comparison of three species: *Brassica oleracea; Avena sativa; Oryza sativa.* Amer. Jour. Bot., 14: 627.

(26) Frank, B. 1887. Ueber Ursprung und Schicksal der Salpetersäure in der Pflanze. Ber. Deut. Bot., 5: 472–487.

(27) Gerneck, R. 1902. Ueber die Bedeutung anorganischer Salze für die Entwickelung und den Bau der höheren Pflanzen. Inaug.-Diss. Göttingen. 148 pp.

(28) Grew, N. 1685. Anatomie des Plants.

(29) Haberlandt, G. 1887. Ueber die Lage des Kernes in sich entwickelenden Zellen. Ber. Deutsch. Bot. Ges., 5: 205–212.

(30) ———. 1887. Ueber die Beziehungen zwischen Function und Lage des Zellkernes bei den Pflanzen. G. Fischer, Jena.

(31) Hansteen, B. 1910. Ueber das Verhalten der Kulturpflanzen zu den Bodensalzen. I, II. Jahrb. Wiss. Bot., 47: 289–376.

(32) Hansteen-Cranner, B. 1914. Ueber das Verhalten der Kulturpflanzen zu den Bodensalzen. III. Jahrb. Wiss. Bot., 53: 536–599.

(33) Hesse, H. 1904. Beiträge zur Morphologie und Biologie der Wurzelhaare. Diss. Jena.

(34) Hill, T. G. 1908. Observations on the osmotic properties of the root hairs of certain salt-marsh plants. New Phytol., 7: 133–142.

(35) Howe, Caroline G. 1921. Pectic material in root hairs. Bot. Gaz., 72: 313–320.

(36) Jeffs, R. E. 1925. The elongation of root hairs as affected by light and temperature. Amer. Jour. Bot., 12: 577–606.

(37) Juel, H. O. 1884. Beiträge zur Kenntniss der Hautgewebe der Wurzeln. Bihang. K. Svenska Vet. Ak. Handlingar, 99: pp. 18.

(38) Kisser, J. 1925. Ueber das Verhalten von Wurzeln in feuchter Luft. Jahrb. Wiss. Bot., 64: 416–439.

(39) Klemm, P. 1895. Des Organisationerscheinungen der Zelle. Jahrb. Wiss. Bot., 28: 626–700.

(40) Kny, L. 1898. Ueber der Ort des Nährstoff-Aufnahme durch die Wurzel. Ber. Deutsch. Bot. Ges., 16: 216–236.

(41) Kraemer, K. 1903. Wurzelhaut, Hypodermis, und Endodermis der Angiospermenwurzel. Bibl. Bot., 12: 1–151.

(42) Krassnow, A. G. 1885. Ueber die Wirkung der Salze der Knopf'schen Nährflüssigkeit auf das Wachstum der Kresswurzel. Arb. Petersbg. Naturf. Ges., 16: 35–37. (Russian)

(43) Kraus, G. 1876. Beobachtungen über Haarbildung zunächst an Kartoffelkeimen. Flora, 59: 153–154.

(44) Kuster, E. 1907. Ueber die Beziehungen der Lage des Zellkernes zur Zellenwachstum und Membranbildung. Flora, 97: 1–23.

(45) Leavitt, R. G. 1902. The root hairs, cap, and sheath of *Azolla*. Bot. Gaz., 34: 414–419.

(46) ———. 1904. Trichomes of the root in vascular cryptogams and angiosperms. Proc. Bost. Soc. Nat. Hist., 31: 273–313.

(47) Lepeschkin, W. W. 1926. Ueber metabolisierte Schichten des Protoplasmas der Pflanzenzellen. Ber. Deutsch. Bot. Ges., 44: 7–14.

(48) Lesage, P. 1891. Contributions à la physiologie de la racine. Compt. Rend. Acad. Sci. Paris, 112: 109–110.

(49) Magowan, Florence N. 1908. The toxic effect of certain common salts of the soil on plants. Bot. Gaz., 45: 45–49.

(50) Malpighi, M. 1686. Opera omnia. De radicibus plantarum, 59–72.

(51) Masters, M. T. 1879. Notes on root hairs and root growth. Jour. Roy. Hort. Soc., 5.

(52) McDougall, W. B. 1921. Thick-walled root hairs of *Gleditsia* and related genera. Amer. Jour. Bot., 8: 171–175.

(53) Mer, E. 1879. Recherches expérimentales sur les conditions de développement des poils radicaux. Compt. Rend. Acad. Sci. Paris, 88: 665–668.

(54) ———. 1880. De la constitution et fonction des poils radicaux. Compt. Rend. Assoc. Franc. l'avancement Sci., 9: 688–695.

(55) ———. 1884. Nouvelles recherches sur les conditions de développement des poils radicaux. Compt. Rend. Acad. Sci. Paris, 98: 583–586.

(56) Meyen, F. J. T. 1838. Neues System der Pflanzenphysiologie 2: 9–14.

(57a) Michels, H. 1920. Note au sujet de l'action des sels de sodium et de potassium sur la germination. Rec. Inst. Bot. Leo Errera, Bruxelles, 10: 161–167.

(57b) Ohlert. 1837. Einige Bemerkungen über die Wurzelgasern der höheren Pflanzen. Linnaea, II, 609.

(58) Ohga, I. 1926. On changes of osmotic pressure in certain plants. Bot. Mag. Tokyo, 40: 587–591.

(59) Osterhout, W. J. V. 1910. On the penetration of inorganic salts into living protoplasm. Zeitschr. Physik. Chem., 70: 408–413.

(60) Patschovsky, N. 1919. Zur Ernährungs-und Entwicklungsphysiologie von *Chara fragilis* Desv. Ber. Deutsch. Bot. Ges., 37: 404–411.

(61) Persecke, K. 1877. Ueber die Formänderung der Wurzel in Erde und Wasser. Inaug. Diss. Leipzig.

(62) Pethybridge, C. H. 1889. Beiträge zur Kenntniss der Einwirkung der anorganischen Salze auf die Entwicklung und den Bau der Pflanzen. Diss. Göttingen.

(63) Pfeffer, W. 1889. Zur Kenntniss der Plasmahaut und der Vacuolen nebst Bemerkungen über den Aggregatzustand der Protoplasmas und über osmotische Vorgänge. Abh. Sächs. Ges. Wiss., 16: 185–197.

(64) Popesco, St. 1926. Recherches sur la région absorbante de la racine. Buletinul Agriculturii, 4: 59–191.

(65) Reinhardt, M. O. 1892. Das Wachstum der Pilzhyphen. Ein Beitrag zur Kenntniss des Flächenwachstums vegetabilischer Zellmembranen. Jahrb. Wiss. Bot., 23: 479–566.

(66) Roberts, Edith A. 1916. The epidermal cells of roots. Bot. Gaz., 62: 488–506.

(67) Sachs, J. 1865. Handbuch der Experimentelle Physiologie. Leipzig.

(68) Sauvageau, C. 1889. Sur la racine du Najas. Jour. Bot., 3: 3–11.

(69) ———. 1889. Contribution à l'étude du system méchanique dans la racine des plantes aquatiques. Les Potomogeton. Jour. Bot., 3: 61–72.

(70) ———. 1889. *Ibid.* Les Zostera, Cymodocea et Posidonia. Jour. Bot., 3: 169–181.

(71) Schaede, R. 1923. Ueber das Verhalten von Pflanzenzellen gegenüber Anilinfarbstoffen I. Jahrb. Wiss. Bot., 62: 65–91.

(72) ———. 1923. Ueber das Verhalten von Pflanzenzellen gegenüber Anilinfarbstoffen II. Ber. Deutsch. Bot. Ges., 41: 345–351.

(73) Schwarz, F. 1883. Die Wurzelhaare der Pflanzen. Unters. Bot. Inst. Tübingen, 1: 135–188.

(74) Seidel, K. 1924. Untersuchungen über das Wachstum und die Reizbarkeit der Wurzelhaare. Jahrb. Wiss. Bot., 63: 501–552.

(75) Snow, Laetitia M. 1905. The development of root hairs. Bot. Gaz., 40: 12–48.

(76) Sokolowa, C. 1897. Ueber das Wachstum der Wurzelhaare und Rhizoiden. Bull. Soc. Imp. Nat. Moscou, 11: 167–260.

(77) Stiehr, G. 1903. Das Verhalten der Wurzelhaare gegen Lösungen. Diss. Kiel.

(78) Strugger, S. 1926. Untersuchungen über den Einfluss der Wasserstoffionen auf des Protoplasma der Wurzelhaare von *Hordeum vulgare* L. (I). Sitzb. Akad. Wiss. Wien, Math-naturw. Kl., 135. 454–478.

(79) Trelease, S. F. and Trelease, Helen M. 1925. Growth of wheat roots in salt solutions containing essential ions. Bot. Gaz., 80: 74–83.

(80) Turina, B. 1922. Vergleichende Versuche über die Einwirkung der Selen-, Schwefel- und Tellursalze auf die Pflanzen. Biochem. Zeit., 129: 507–533.

(81) Ursprung, A. and Blum, G. 1921. Zur Kenntniss der Saugkraft V. Ber. Deutsch. Bot. Ges., 39: 139–148.

(82) van Tieghem, Ph. 1887. Sur les poils radicaux gémines. Ann. Sci. Nat. Bot. VII, 6: 127–128.

(83) Vöchting, H. 1902. Ueber die Keimung der Kartoffelknollen. Bot. Zeit., 60: 87–114.

(84) Watson, E. E. 1919. On the occurrence of root hairs on the old roots of *Helianthus rigidus*. Michigan Acad. Sci. Ann. Rept., 21: 235.

(85) Went, F. A. F. C. 1894. Ueber Haft-und Nahrwurzeln bei Kletterpflanzen und Epiphyten. Ann. Jard. Bot. Buitenzorg, 12: 2–12.

(86) Whitaker, Edith S. 1923. Root hairs and secondary thickening in Compositae. Bot. Gaz., 76: 30–59.

(87) Windel, E. 1917. Beziehungen zwischen Function und Lage des Zellkernes bei Wurzelhaare. Beih. Allg. Bot., 1: 45–93.

(88) Wortmann, J. 1889. Beiträge zur Physiologie der Wachstum. Bot. Zeit., 47: 277–286.

(89) Zacharias, E. 1891. Ueber das Wachstum der Zellhaut bei Wurzelhaaren. Flora, 74: 466–491.

(90) Ziegenspek, H. 1920. Das Amyloid jugendlicher Organe. Das Amyloid in der wachsenden Wurzelhaaren und seine Beziehungen zum Zellwachstum. Ber. Deutsch. Bot. Ges., 38: 328–333.

(91) ———. 1927. Die Lage des Zellkernes in den Wurzelhaaren von *Hydrocharis morsus ranae* während des Wachsens. Arch. Bot. (Königsberg), 20: 475.

CONTROLLED MATING IN HONEYBEES

By LLOYD R. WATSON

Department of Plant Breeding, Cornell University

BEEKEEPING has been practiced for more than three thousand years, and more books and treatises have been written about bees than about any other farm animal, the horse and the fowl not excepted; yet practically no progress has ever been made in improving the types of these useful insects.

The great handicap to bee culture of all time is that it has never been possible to breed bees in the direction of desired varieties, as is done with cattle, sheep, poultry and all ordinary domestic animals, for the reason that the mating of the queenbee with the male takes place high in the air and free on the wing, where it cannot be controlled. She consistently chooses to manage her own nuptials to suit herself, free from human interference, instead of accepting whatever mate the beekeeper, alert for improvement of the bee population, wishes to select for her. Because the beekeeper has in the past been unable to control the male parentage of his bees, breeding for the improvement of the honeybee along scientific lines has been practically impossible.

Honeybees are not indigenous to America. It has therefore come to pass that the bees now found in this country are genetically a very heterogeneous group which has resulted from the endless crossing and intercrossing of the progeny of the numerous varieties which have been brought here, principally from the lands bordering upon the Mediterranean sea. It is true that more or less distinct varieties of honeybees exist in their own respective habitats. Thus, the native bees of Carniola, Italy, Cyprus and Caucasia constitute our most clearly defined and best known types. All of these varieties readily hybridize among themselves when the opportunity is given, and it seems certain that geographical barriers such as waters, mountains and deserts have made possible, first the evolution of these varieties, and finally their preservation through many centuries.

MATING HABITS OF HONEYBEES

The queenbee is normally fecundated by a single drone, and in the air, during her once-for-life nuptial flight. How important a part the ability to fly plays in the life of bees is intimated in the fact that queens and drones that do not possess strong, perfect wings may not hope ever to function in the perpetuation of their race.

The blind scientist, Huber, ascertained (1791) that a single mating is sufficient to fertilize all the eggs that a queen will lay in the course of two years at least, and it has later been demonstrated that this influence will last throughout the course of her whole life, which may be from three to seven years. In a few rare instances queens have been known to mate on two successive days, probably because the first mating was insufficient,

but these exceptions are so few as almost to prove the rule.

The reproductive organs of the queen-bee consist of two gigantic ovaries whose ducts, leading backwards, coalesce into a single canal, the oviduct, which hastens to its exit in the genito-anal vestibule (fig. 1). At a slight distance from the vestibule, and on the dorsal side of the oviduct, is a tiny spherical pouch opening into the latter. This is the spermatheca, the exact function of which sorely vexed the early students of insect physiology.

The gropings of the early investigators after the true explanation of how bees' eggs are fertilized, and how a queen can lay two kinds of eggs apparently at will,

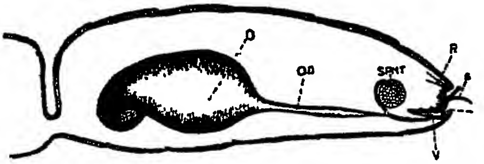


FIG. 1. FREE-HAND SKETCH OF QUEEN'S ABDOMEN

Conventionalized side view showing relative position of the reproductive organs only; *o*, left ovary; *od*, oviduct; *spmt*, spermatheca; *v*, vulva; *r*, rectum; *s*, sting; *vb*, vestibule.

constitute a long but engaging story. After years of health-breaking study, during the course of which he recorded many, but obviously not all, of the critical habits of the hive, Swammerdam concluded (1673) that queenbees were not fecundated by actual physical contact with the drones because, he said, the generative organs of the drones were quite too large. Led by the observation that when drones are shut up in a small space, as a bottle, they exhale a characteristic body odor, which he conceived to be an emanation of the "*aura seminalis*," or the *aura seminalis* itself, he concluded that in the hive this aura penetrated the body of the queen and effected fertilization. He believed that the spermatheca contained a mucilaginous secretion for sticking the eggs to the bottom of the cells.

Swedenborg believed (1750) that all the eggs of bees were unfertilized when laid, but that later the eggs in the cells were visited by the drones and fertilized individually by a contact process. Réaumur, the inventor of the thermometer which bears his name, announced (1740) that the true function of the spermatheca is to receive and hold the fertilizing material from the drone, and to deal it out, a few sperms at a time, to the eggs as they pass down the oviduct.

It remained for Dr. John Dzierzon (1845) to make his illuminating contribution, the theory of parthenogenesis, and to apply it to honeybees. This theory has never had to be changed. Substantiated by every conceivable proof, and amplified by more recent findings, the case of honeybees may now be stated as follows: all the eggs of the queenbee are unfertilized as they leave the ovaries, and they are potentially only male producing. The chorion of these unlaid eggs contains near the large end a tiny hole, the micropyle, through which a sperm may enter as the egg descends the oviduct and passes the spermathecal duct. The fusion of the sperm cell with the nucleus of an egg constitutes the fertilization of the egg, and when it hatches a female bee results. Drones have never been known to develop from fertilized eggs. But discharging eggs do not always receive a sperm as they pass the spermatheca, and such eggs are never fertilized. When hatched they can produce only drones.

The queen is the only perfect female in the hive, and her sole function is to recruit the family. The workers are also females, and are reared from the same kind of eggs, viz., fertilized eggs, but owing at least in part to the kind of food given them during the larval stage their genera-

tive organs are so dwarfed and imperfect that they cannot mate with a drone, and drones are never seen to badger worker-bees. Under certain conditions the ovaries of some workers may be developed sufficiently to enable them to lay eggs which will hatch and mature, but like those of a virgin queen, their eggs can produce only drones.

THE QUEENBEE CONTROLS THE SEX OF HER OFFSPRING

Voluntary control of the sex of the offspring is a unique gift of Nature, which is enjoyed by the queenbee. This ability is possessed by extremely few, if indeed by any other, insects, and probably for sound reasons it has never been entrusted to the hands of Man. We lack definite information as to how the queen controls the fertilization of her eggs. The feat of laying two thousand eggs a day, as she sometimes does, and of properly distributing them with almost unerring precision, the fertilized ones in worker-cells, and the unfertilized ones in the larger drone-cells, places a tremendous burden of presumption upon the discrimination of the queen.

If the fertilization of the eggs were to occur in a hit-and-miss fashion as they descend the oviduct and pass the spermatheca, then we should expect to see the queen oscillating back and forth more or less at random between the worker-comb and the drone-comb to enable her to place the eggs properly. This does not occur, and our difficulty in attempting to discredit the "will" of the queen in controlling the fertilization of her eggs is further sharpened by the classical observation that a normal queen lays eggs appropriate to the kind of comb she is on. Thus, she never seems to be obliged to leave a worker-comb for instance, and go over to a drone-comb so that she can dispose of an unfertilized egg or two before she can proceed with the laying of more fertilized eggs. The burden of precision would seem not to rest in some faculty of the queen by which she knows whether the next to be laid will be a fertilized egg or an unfertilized one; nor can it rest in any mechanics of the cell, as if its shape or size or depth were determining factors, for prolific queens sometimes follow upon the heels of the comb-builders so closely that eggs are deposited when the cells are only a third completed. Furthermore, when in the economy of the hive drones are desired, and no drone-comb is available, she does not hesitate to deposit unfertilized eggs in worker-comb. Rather does the burden of precision appear to rest in a voluntary control of the mechanism of the spermathecal duct which parcels out fertilizing material to some eggs as they pass, and not to others, depending upon the season, the condition of the colony, and the hereditary complex of the queen. Students of insect psychology are reluctant to concede voluntary acts to insects, and the concession is allowed in this case only as a makeshift till further investigations shall bring forth a more satisfactory explanation.

It has been supposed that a mated queen could continue to lay fertilized or unfertilized eggs at will just as long as there were any sperms left in the spermatheca, but this is not strictly the case. Long before the supply of sperms has been completely exhausted most queens begin to deposit a larger and larger proportion of unfertilized eggs, and as a classical symptom of approaching sterility or decrepitude in the queen these unfertilized eggs are scattered about in worker-cells.

In the phraseology of human psychology, therefore, the situation might be stated about as follows: she willed to lay

a fertilized egg, and she tried to do so, but because of the thinning out of the sperms in the fluid within the sperm reservoir, the normal draught made upon the spermatheca for fertilizing material with which to bathe the micropyle of a passing egg contained no sperms, or it contained so few that none of them found the open micropyle, and the egg got by without being fertilized. Now, having called upon her determining mechanism for a fertilized egg, she treats the resulting ovum as if it were what she ordered, and places it in a worker-cell. Thus, the presence of drone-brood scattered among worker-brood is not referable to any fault of her will, but to the exhaustion of her stock of sperms. Workerbees appear to be able to discriminate instantly between fertilized eggs and unfertilized ones, but there is no data to warrant one in attributing any such ability to queenbees.

For obvious reasons copulation in honeybees has very rarely been observed, but from the few reported observations, and more especially from the examination of queens just returning from the wedding flight we establish that the rapidly flying virgin queen is pursued by many competing consorts. The strongest drone, outflying most of his rivals, and parrying with the few, maneuvers into a position ventro-ventral with the queen. They grasp each other while still flying, the main axes of their bodies being in a position parallel to each other and usually perpendicular to the earth. In this condition copulation occurs. After normal copulation the drone is unable to extricate his organ from the vulva of the queen, and it is torn from him altogether. It is borne home by the queen and retained by her till its contents have found their way into the oviduct, after which it is dropped as a dry shred. The spermatozoa now separate themselves from the seminal fluid in the oviduct and, stimulated perhaps by chemotaxis, migrate into the spermatheca. Here they remain alive and active for months or years apparently without the taking of any nourishment, for which they have no known morphological capacity, or until they are called to leave again by the same route by which they entered.

MANY ATTEMPTS TO CONTROL MATING

The desirability of some means of controlling the mating of the queenbee has been recognized for more than a century and a half, and skilled experimenters in many lands have not ceased to attack the problem by every conceivable approach. The known attempts to accomplish this end readily fall under two general heads: (1) the isolation of the virgin queen with one or more selected drones in a limited range, and (2) forced insemination by violent or by surgical means. The following list of methods which have been tried by outstanding experimenters is by no means complete, but it is representative:

(1) Painting the vulva of the queen with fresh sperm,

(2) Queen tied out on a leash,

(3) Queen confined with selected drones in a limited range such as wire cages, small glass enclosures, immense greenhouses, on islands, and in localities uninhabited by other bees,

(4) Dropping seminal fluids into the open vulva of the queen,

(5) Queen and drone held in juxtaposition,

(6) Painting unfertilized eggs with sperm,

(7) Queen held in a block and injected.

So far as we know none of the methods catalogued above have proved to be practical for scientific or for commercial

use, except the last one, and in our own laboratory.

The artificial introduction of semen into the reproductive tract of certain of the warm blooded animals has been practiced for a long time, and the principle is scientifically sound. Prior to these investigations, however, this principle had never been successfully applied to insects. Their small size presented a baffling difficulty, but in the event that the technique could be refined sufficiently, the question still remained: does the drone merely deposit the spermatozoa within the oviduct of the queen, leaving them to make their way as best they can up the curving duct into the sperm reservoir, or does he reach farther and deliver them under compression directly into the spermatheca? The answer to this question was established by the dissection and examination of many naturally mated queens as they returned to the hive after the wedding flight.

The office of the drone in mating appears to be merely to deposit the tiny charge of semen within the oviduct of the queen. Immediately after this for the next four to seven hours, and stimulated by some force which is not fully understood, the individual spermatozoa, numbering perhaps a million or more, set up a powerful lashing of their flagella by means of which they work their way up the duct, and collect at last in the spermatheca.

A critically important item relating to the physiology of copulation in honeybees should be mentioned here. Queens freshly mated, as they return to the hive, are observed always to bear in the genito-anal vestibule a copious mass of mucus from the accessory mucous glands of the male. The function of this mucus is to harden in contact with the air, and be a sort of plug to close the vulva, preventing the back flow of the semen, and protecting it from exposure to the air. It has been established by repeated experiments that if the mucous plug is torn away from a normally mated queen, or even slightly meddled with before she has borne it for two or three hours, she may be temporarily or permanently incapacitated to lay fertile eggs.

THE APPARATUS

The insemination of a queenbee is by nature a microscopic operation, and a binocular microscope giving a magnification of 15 to 18 diameters is indispensible. An all-glass syringe convenient for handling the tiny bead of semen from a single drone seems not to be made commercially anywhere, and we are compelled to design and construct our own. The critical specifications of this syringe are (1) a straight, all-glass plunger barrel of perfectly uniform bore 0.5 millimeter in inside diameter, and (2) a tight fitting plunger controlled by a fine-threaded screw allowing a plunger stroke of 15 to 20 millimeters.

A consideration of first magnitude in this work is that every movement shall be under perfect control. To control and stabilize the movements of the micro-syringe, this instrument is clamped in the jaws of a Barber pipette-holder (fig. 2). The turning of one or another of the three nurled screwheads set at right angles to each other in the three planes of space slowly moves the syringe forwards and backwards, up and down, right and left. This micromanipulator is mounted on a flange which rises from a false stage fitted over the real stage of the microscope, and is tilted so as to incline the syringe at an angle of about 40 degrees to the horizontal, thus permitting the operator to look into the vestibule of the queen while emplacing the syringe.

The queen also must be securely held

perfectly motionless to prevent her from injuring herself by struggling. With careful handling she is placed dorsal side downward in a form carved out of a small block of wood (fig. 3) just to fit her thorax, head and abdomen, with the tip of the abdomen extending slightly over the edge of the wood. Furthermore, this little operating-table tilts her up so that the long axis of her body is in direct line with the long axis of the microsyringe. She is held motionless in this position by several strands of silk thread thrown over her body and around the operating-table. Much caution is needed to insure that her wings and legs are in comfortable position, for if she should emerge from the ordeal with twisted legs or crumpled wings she would not be acceptable to the bees.

A strong, steady light is needful to facilitate work on dull days and at night, but it is unwise to let strong artificial light shine directly upon the queen, or upon the spermatozoa. We employ a shaft of parallel light from a 150-watt microscope lamp, reflected and focused by a concave mirror, but we do not expose her to this intense light for long at a time.

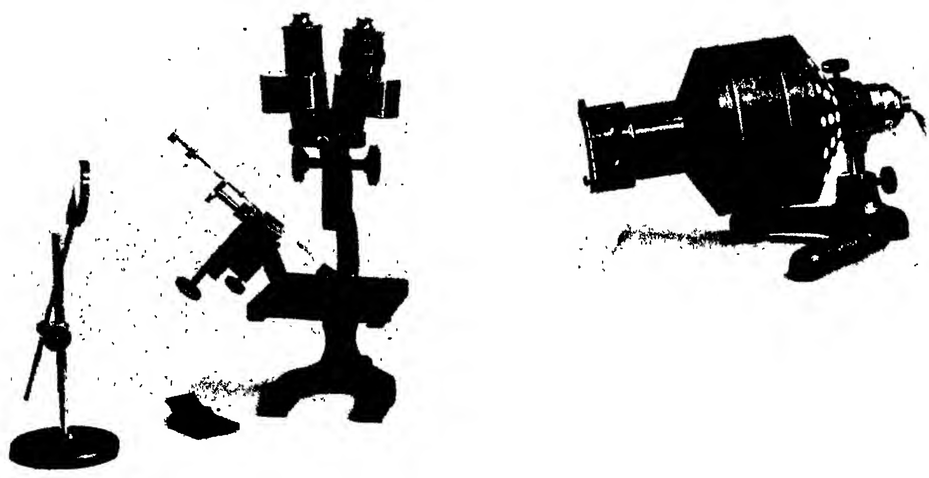


Fig. 2. Showing the Position of the Apparatus Ready for Work

THE TECHNIQUE

A few minutes before tying the queen down we liberate a few choice drones on the inside of the window. The strongest ones demonstrate their strength by flying hardest and longest against the pane, while the weak and immature ones settle down soon to rest at the bottom of the window. While this assorting of the drones is in progress we lightly seize the virgin queen to be injected, make her fast in the form on the operating-table, and set her aside to wait while we fill the syringe. If she has been out of the hive very many minutes she is hungry, and she will probably accept a taste of thin honey given to her on a toothpick as she waits.

From the few drones still flying on the window we seize one of the most vigorous fellows, and clip off his head. The shock of decapitation will probably cause him to evert the copulatory organ more or less

completely. Sometimes merely seizing a drone, or lightly twirling him in the fingers will cause him to react in this way. If decapitation does not cause him to ejaculate he is discarded, and another one is tried. When the desired reaction

FIG. 3. THE OPERATING-TABLE, NATURAL SIZE
The cradle exactly fits the head, thorax and abdomen of the queen

is obtained (fig. 4), we grasp the everted curved organ with sharp tweezers and pull it loose from the body. With the penis is brought away also the so-called bulb or seminal pouch swollen with its

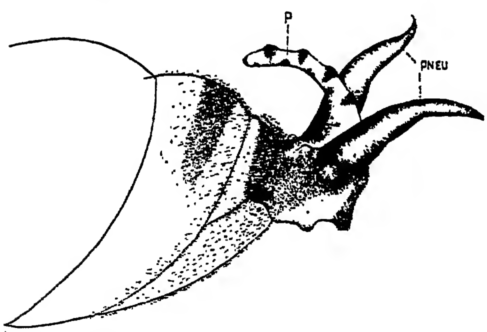


FIG. 4. SHOWING THE GENITALS OF THE DRONE AS THEY APPEAR AT THE MOMENT OF EJACULATION
P, penis; *pneu*, pneumophyses

tiny charge of creamy colored sperm and pearly white mucus (fig. 5).

With sharp scissors we snip off the ejaculatory duct at the point where it begins to widen to form the bulb, quickly lay the detached bulb on the index finger of the left hand, and pass it into the magnified field of the binocular. The separate regions of the mucus and of the sperm are now easily distinguished by their colors, and the degree of magnification suggested above readily permits the operator to observe the swirling masses of spermatozoa through the thin walls of the bulb.

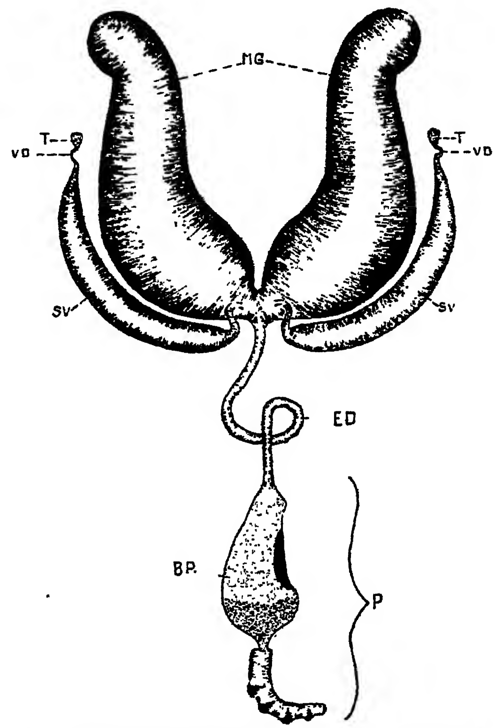


FIG. 5. REPRODUCTIVE ORGANS OF A FULLY MATURE DRONE, PARTIALLY CONVENTIONALIZED
Showing relative position after ejaculation has been induced and the organs have been pulled away with the tweezers. *Mg*, accessory mucous glands; *sv*, seminal vesicles; *vd*, vas deferens; *t*, testicle; *ed*, ejaculatory duct; *p*, penis; *bp*, bulb of the penis. Note that the pneumophyses are left behind with the abdomen. The regions of the sperm and of the mucus in the bulb, *bp*, are clearly visible.

The finger is now moved forward so that the tip of the syringe is made to enter the region of the white mucus through the opening where the ejaculatory duct was cut off. The plunger is screwed back about two millimeters, thus taking up a little of the mucus. The finger is then advanced slightly so as to bring the point

of the syringe into the midst of the yellow sperm. This is about all taken up, leaving the collapsed bulb nearly empty. The virgin queen still resting on the operating-table, and having been fed, is now brought into the magnified field, and placed with the tip of the abdomen in the center of the field, and pointing toward the syringe. The operating-table is made fast in this position by a rubber band passing over it and underneath the table.

The left hand grasping a pair of the finest pointed tweezers, and the right hand holding some moderately sharp applicator, such as a dissecting needle, now coöperate to pry apart the genito-anal plates of the queen, an operation which some queens resist with remarkable force. The tweezers are gently maneuvered into such position that when allowed to open slightly they push back the plates, and expose to view the sting, sting palps, rectum and vulva. While the left hand holds the vestibule open (fig. 6) with the tweezers, the right hand operates the controls of the micromanipulator so that the tip of the syringe stands just over the opening of the oviduct, and then enters it to the depth of about a millimeter. The plunger is now slowly advanced till the semen is all deposited within the queen. Finally, as the syringe is backed away, the droplet of mucus which, it will be recalled, was taken up ahead of the semen in loading, is the last to be discharged, and is left to thicken in and over the vulva as a plug to prevent any back flow and to shut out the air.

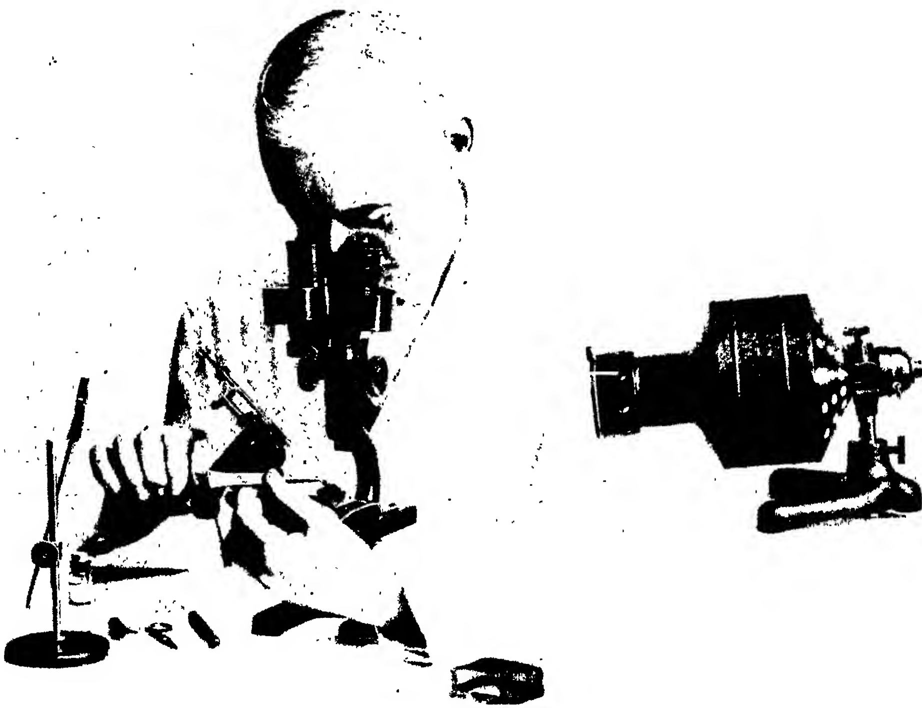


Fig. 6. Showing the Position of the Operator While at Work
Both elbows rest on the desk, and the left hand is further steadied against the stage of the microscope

The queen may now be released from the operating-table, both wings on one side clipped off to prevent any subsequent flight in pursuit of further nuptials, and then returned to her own bees. If she received no injuries during the operation she will be accepted by her own bees with the same etiquette as if she were only returning from a natural wedding flight. If all is well she will begin oviposition in a day or two, and follow in every respect thereafter the rôle of a normally mated queen.

Instrumental insemination of queenbees is in its infancy. Its first birthday has just passed. Successful queens began to appear in the autumn of 1926. Because of the lateness of the season it was not possible to culture many of the treated queens through a complete life cycle before winter. Data as to the success or failure of the operation, therefore, were gathered from about 40 of the treated queens by determining the presence or absence of spermatozoa in the spermatheca under dissection. Somewhat more than 50 per cent of the queens examined were found to have received insemination ranging all the way from very slight up to normal.

MATURE DRONES NECESSARY FOR SUCCESS

Let it be recalled that the spermatheca of a virgin queen contains only a thin, clear liquid, but that after successful insemination, either natural or instrumental, this liquid appears thick and opaque because of the million or more of spermatozoa suspended in it. The mating of a normal queen with a vigorous drone results in the dense crowding of the sperm reservoir with motile sperms, but if the mating occurs with a less vigorous male the number of sperms received may be very much less, and her period of usefulness as a layer would obviously be proportionately shorter. To enable her to head a populous colony successfully for the usual span of two or three years, it is necessary that the queen should have the most copious insemination possible in the beginning, because (1) queens do not take mating flights on successive years to replenish their stock of sperms, and (2) there is no multiplication of sperms within the spermatheca.

Whether a queen that has received scant insemination, either on the wing or under the microscope, will attempt to make subsequent flights in pursuit of further nuptials seems not to be governed by any regularity which we now understand. Some queens that have received insemination equal only to about 5 per cent of the normal degree never show any desire to mate again, but turn themselves at once to a rapid but brief period of egg laying; other queens that have received as much as 50 per cent of the normal amount of insemination never lose the passion to get out on the wing and mate again.

BETTER EQUIPMENT NEEDED

The second season of instrumental insemination has seen no great changes in the equipment used nor in the method of using it. Some improvement in technique is suggested by the fact that the proportion of queens receiving some degree of insemination has risen from 50 per cent in 1926 to 65 per cent in 1927. The need has been felt for a more convenient and more adaptable form of operating-table, and designs are incubating for a perfectly stabilized retracting device to hold open the genito-anal vestibule of the queen while the syringe is being emplaced. Especially is it to be desired to have this function performed under better control than is possible by the pulsating left hand of the operator.

PRESENTATION OF DATA

Brief inspection of the following data taken from the records of 1927 serves to show how subtle are some of the factors dealt with in the problem of controlled mating of these insects. In all 96 virgin queens were treated from once to ten times each depending upon their behavior. To prevent their leaving the hive at any time in pursuit of natural mating the hive entrances were always closed with perforated zinc which allows workers to pass in and out freely, but will not allow queens and drones to pass. If a treated queen was seen trying to leave the hive she was taken to the laboratory and treated again. Thus, some queens were fully inseminated as the result of one injection, and one queen is known to have received only 50 per cent normal insemination after nine injections. To ascertain at once the extent of insemination the spermatheca was dissected out and crushed under a microscopic cover slide. The degree of insemination was then estimated in per cent of the normal.

Of the 96 queens that were treated 66 per cent received an appreciable degree of insemination and 34 per cent received no sperms into the spermatheca. Furthermore, of all the queens that received an appreciable degree of insemination,

79% received 5% normal insemination or more
38% received 10% normal insemination or more
17% received 50% normal insemination or more
11% received 75% normal insemination or more
6% received 100% normal insemination

During the course of the season several promising queens disappeared for one cause or another before any brood was produced, and there was no means of determining whether they would have been successes or not. In making the records such missing queens were counted as total failures although probably some of them were inseminated.

To estimate the degree of insemination of queens that are still living, note was taken of the percentage of worker-brood produced by them. For example, if 10 per cent of her brood was sealed flat by the workerbees, and the rest was sealed oval, a queen was estimated to have received about 10 per cent of the normal degree of insemination. The absence of any oval, or drone-brood, was taken to mean that her insemination was normal. This method of arriving at the results of treatments is obviously open to criticism. However, during the first few weeks of her life as a laying queen, and especially when a treated queen is being cultured in a nucleus, there has been found to be a remarkably close correlation between the degree of her insemination and the proportion of fertilized eggs that she lays.

WHY ARE RESULTS SO VARIABLE?

That instrumental insemination of queen-bees is still in the experimental stage is evidenced by the large proportion of queens that receive only partial insemination as the result of a single injection. It still frequently happens that when half a dozen queens from the same hatch are treated exactly alike on the same day, some will be copiously inseminated while others are complete failures. Repeated injections build up the degree of insemination, but repeated injections are impractical in most hereditary studies. Queens that have received less than 10 per cent normal insemination cannot be depended upon to settle themselves to oviposition; however, as low as 5 per cent of worker-brood may be quite sufficient to enable valuable genetical studies to be made. To the question, why are the results so variable, we are compelled in candor to answer that we do not yet know.

In systematic search for an underlying cause of such wide differences in results, both the technique and the general condi-

tions of the experiment have been varied within wide limits. The size of the dose of seminal fluids injected has been varied; some queens have been injected rapidly, and others very slowly; the exposure of the seminal fluids to sunlight, to artificial light, and to heat and cold has been widely varied; some queens have been injected when only seven days old, while others were allowed to attain the age of fifty days before being treated; with some queens the dose consisted of nearly pure sperm with almost no admixture of mucus, with others of a loose mixture of sperms and mucus; sometimes the dose was made to consist of a suspension of semen in normal physiological saline solution, and sometimes of a mixture of semen from several drones all at once. So far these variations of procedure have not led to the uncovering of any certain cue, in either a positive or a negative way.

DRONES SUSPECTED OF INFERTILITY

The condition of the problem at the present time casts a glance of suspicion toward the drone. A fund of evidence has accumulated which lightly points to the possibility that partial or complete sterility of the drones may be the variable factor; that motility of the sperms is not a dependable criterion by which to judge of their functional maturity. More and more we find ourselves selecting for laboratory use the oldest drones obtainable. Furthermore, there is little evidence to warrant the assumption that all the drones that ejaculate when decapitated are functionally mature. When we can have them, we prefer drones that ejaculate vigorously when merely seized and gently twirled between the thumb and fingers. Every beginning is a struggle against inertia, but a beginning has been effected, and the problem bristles with genetical and economic possibilities.

OTHER SCIENTISTS SUCCESSFULLY REPEAT THE EXPERIMENT

Developments to the present time confirm the belief that the principle of instrumental insemination is practical as a means of controlling the mating of honeybees. The trend of the technique is in the direction of greater simplicity, the actual operation being somewhat simpler now than was at first thought possible. Several experimenters after witnessing a few demonstrations have been able to take the equipment and inseminate queens for themselves. This fact must not be interpreted to mean that instrumental insemination in its present development is adapted to the immediate use of workers untrained in microscopic technique. In the hands of a microscopist, however, the operation is very simple.

HONEYBEES PROMISE TO BE VALUABLE MATERIAL FOR GENETIC RESEARCH

Perfect control of mating in honeybees places the new science of honeybee eugenics in the biological curriculum. An attractively large number of the qualities necessary for ideal material upon which to make genetical researches are present in honeybees. The following may be mentioned: (1) The life cycle is short; three or more generations may be reared in one season. (2) A single mating gives a large amount of progeny. (3) Bees are large enough to permit much scrutiny without the use of microscopes. (4) The present known measurable hereditary characters of bees are not very numerous, yet there is reason to expect that many more such characters will be discovered when bees are more carefully scrutinized. (5) Bees are hardy; they are easily cultured, and due to their agricultural relationships, any race betterment achieved

with them would have immediate economic value. (6) Finally, the fact that all the eggs of honeybees are potentially parthenogenetic after maturation should serve to simplify certain genetical methods.

The first task in attacking a problem in genetical analysis is to determine whether the parent stocks which are to be used are homozygous for the characters to be studied. Nearly all of the breeding experiments so far performed have, therefore, been directed toward this end. Let it be reiterated that American honeybees are extremely heterozygous. A task of considerable dimensions looms ahead of segregating and stabilizing pure strains of the types we design to work with. The pursuit of this problem during the past season was made possible by the award of an August Heckscher Research Assistantship under Dr. R. A. Emerson in the Plant Breeding Department at Cornell University. A beginning has been made with five of the best defined varieties of bees as follows: golden Italian, Carniolan, Caucasian, Black (German) and so-called Albino.

ONE QUEEN INSEMINATED FROM ANOTHER QUEEN

The mention here may be appropriate of a new experiment which was performed during the past season. This consisted in inseminating a virgin queen with sperm dissected from the spermatheca of a mated queen. Number 38 was a black virgin queen who on her twenty-fourth day was injected with sperm taken from the sperm reservoir of a golden queen who had been mated on the wing some weeks before, and who appeared normal in every way, but who never laid well. Two days later number 38 was dissected and found to have received a slight but certain degree of insemination. This experiment admittedly partakes of the nature of a laboratory curiosity, but the pure science of today sometimes becomes applied science tomorrow.

LIST OF LITERATURE

Alley, Henry. 1893. Thirty Years among the Bees. pp. 1–88.

———. 1885. The Beekeepers' Handy Book. pp. 1–184.

Babcock and Clausen. 1918. Genetics in Relation to Agriculture. pp. 1–675.

Bishop, G. H. 1920. Fertilization in the honeybee. Jour. Exp. Zool., v.31, pp. 225–286.

Cale, G. H. 1926. The first successful attempt to control the mating of queen bees. Amer. Bee Jour., v. 66, pp. 533–534.

———. 1927. Controlled mating of queen bees established on a workable basis. The Bee World, v. 8, pp. 100–102.

Casteel, D. S. 1912. The behavior of the honeybee in pollen collecting. U. S. Bur. Ent. Bull. 121, pp. 1–36.

Castle, W. E. 1924. Genetics and Eugenics. pp. 1–395.

Cheshire, F. R. 1886. Bees and Beekeeping. v. I, pp. 1–336.

———. 1888. Bees and Beekeeping. v. II, pp.

Comstock, A. B. 1920. How to Keep Bees. pp. 1–230.

Cook, A. J. 1883. The Beekeepers' Guide. pp. 1–337.

Cowan, T. W. 1911. British Beekeepers' Guide Book. pp. 1–226.

———. 1904. The Honey Bee. pp. 1–220.

Doolittle, G. M. 1889. Scientific Queen Rearing. pp. 1–169.

Dzierzon, John. 1861. Rationelle Bienenzucht. Transl. by Dieck and Shuttered, 1882. pp. 1–350.

Gage, S. H. 1920. The Microscope. pp. 1–472.

Galiperin, V. 1913. (On the question of the artificial fertilization of the queenbee.) Věstn. Obšč. Pcelŏ. v. 20, pp. 68–76.

Gooderham, C. B. 1923. Bees and how to keep them. Dom. of Can., Dept. of Agr. Bull. 33, new series, pp. 1–60.

Huber, F. 1792 and 1814. Observations on Bees. Transl. by C. P. Dadant, 1926, pp. 1–230.

Hommel, R. 1922. Apiculture, pp. 1–494.

Hunter, J. 1884. A Manual of Beekeeping. pp. 1–218.

Hunter, J. 1792. Observations on bees. Phil. Trans. Roy. Soc., London, Abridged, v. 17, pp. 185–188.

Hutchinson, W. Z. 1918. Advanced Bee Culture. pp. 1–205.

Hutson, Ray. 1926. Relation of the honeybee to fruit pollination in New Jersey. N. J. Agric. Exp. Sta. Bull. 434, pp. 1–32.

Jager, Francis. 1923. Habits and activities of bees. Univ. of Minn. Spec. Bull. 73.

Lamb, C. G. 1922–23. The geometry of insects pairing. Proc. Roy. Soc., 94B, pp. 1–11.

Langstroth, L. L. 1870. The Hive and Honey Bee. pp. 1–409.

Langstroth, L. L., and Dadant, C. P. 1922. The Honeybee. pp. 1–438.

Lineburg, B. 1924. The feeding of the honeybee larvae. U. S. Dept. Agr. Bull. 1222, pp. 25–37.

Loeb, Jacques. 1913. Artificial Parthenogenesis and Fertilization. pp. 1–312.

Lovell, J. H. 1909–10. The color sense of the honeybee. Amer. Nat., v. 43, pp. 338–349 and v. 44, pp. 673–692.

Ludwig, P. A. 1922. Unsere Bienen. pp. 1–448.

Mahin, M. 1880. Improvement of bees. The Beekeepers' Mag., v. 8, pp. 10–11.

McIndoo, N. E. 1914. The olfactory sense of the honeybee. Jour. Exp. Zool., v. 16, pp. 265–346.

———. 1914. The scent producing organ of the honeybee. Proc. Acad. Nat. Sci. Phila., v. 66, pp. 542–555.

———. 1916. The sense organs of the mouthparts of the honeybee. Smithsonian Misc. Col., v. 65, No. 14, pp. 1–55.

———. 1922. The auditory sense of the honeybee. Jour. Comp. Neur., v. 34, pp. 173–199.

1917. Recognition among insects. Smithsonian Misc. Col., v. 68. No. 2, pp. 1–78.

Miller, C. C. 1920. Fifty Years among the Bees. pp. 1–328.

Morgan, T. H. 1919. The Physical Basis of Heredity. pp. 1–305.

Nelson, J. A. 1915. The Embryology of the honeybee. pp. 1–282.

———. 1924. Morphology of the honeybee larva. Jour. Agr. Res., v. 28, No. 12, pp. 1167–1214. 8 plates.

Nelson, J. A., and Sturtevant, A. P. 1924. The rate of growth of the honeybee larva. U. S. Dept. Agr. Bull. 1222, pp. 1–24.

Newell, Wilmon. 1915. Inheritance in the honeybee. Science, N. S., v. 41, No. 1049, pp. 218–219.

Newman, T. G. 1882. Bees and Honey. pp. 1–154.

Nolan, W. J. 1924. Egg-laying rate of the queenbee. Gleanings in Bee Culture, v. 52, pp. 428–431.

———. 1925. The brood-rearing cycle of the honeybee. U. S. Dept. Agr. Bull. 1349, pp. 1–55.

Park, O. W. 1923. The language of bees. Amer. Bee Jour., v. 63, p. 227.

———. 1923. Communication among bees. Amer. Bee Jour., v. 63, p. 449.

———. 1923. Flight studies of the honeybee. Amer. Bee Jour., v. 63, p. 71.

———. 1923. The temperature of the bee's body. Amer. Bee Jour., v. 63, pp. 232–234.

Parker, R. L. 1923. Some pollens gathered by bees. Amer. Bee Jour., v. 63. pp. 16–19. (Abstract of thesis.)

Parks, H. B., and Alex, A. H. 1925. Suggestions on queen rearing. Texas Agr. Exp. Sta. Cir. No. 35, pp. 1–19.

Pellett, F. C. 1915. Productive Beekeeping. pp. 1–302.

———. 1918. Practical Queen-rearing. pp. 1–105.

Perret-Maisonneuve. 1926. L'Apiculture intensive et L'Elevage des reines. pp. 1–550.

Phillips, E. F. 1919. Beekeeping. pp. 1–457.

———. 1905. The rearing of queenbees. Bur. Ent. Bul. 55, pp. 1–32.

———. 1903. A review of parthenogenesis. Proc. Amer. Phil. Soc., v. 42, pp. 275–345.

———. 1905. Structure and development of the compound eye of the honeybee. Proc. Acad. Nat. Sci. Phila., v. 57, pp. 127–157.

———. 1924. The digestion of the honeybee. Gleanings in Bee Culture, v. 52, pp. 52–76.

———. 1922. The effect of activity on the length of life of honeybees. Jour. Econ. Ent., v. 15, pp. 368, 370, 371.

———. 1927. The utilization of carbohydrates by honeybees. Jour. Agr. Res., v. 35, No. 5. pp. 385–428.

———. 1922. The ability of queen and drone honeybees to feed themselves. Jour. Econ. Ent., v. 15, pp. 430–432.

Prath, O. E. 1924. Do anesthetized bees lose their memory? Amer. Nat., v. 58, No. 655, p.162.

Pratt, E. L. 1904. Baby Nuclei. pp. 1–34.

———. 1905. Commercial Queen Rearing. pp. 1–42.

———. 1906. Simplified Queen Rearing. pp. 1–26.

———. 1906. Forcing the Breeding Queen to Lay Eggs in Artificial Queen-cups. pp. 1–28.

Prell, H. 1927. Die künstliche Befruchtung der Bienenkönigin. Sonderabdruck aus der Märki-

schen Bienenzeitung, Jahrgang 1927. Nr. 10. pp. 1–5.

QUINBY, MOSES. 1865. Mysteries of Beekeeping Explained. pp. 1–348.

ROOT, A. I., and ROOT, E. R. 1923. ABC and XYZ of Bee Culture. pp. 1–960.

ROOT, H. H. 1910. Alexander's Writings on Practical Bee Culture. pp. 1–98.

ROOT, L. C. 1918. Quinby's New Beekeeping. pp. 1–271.

SHAFER, G. D. 1917. A study of the factors which govern mating in the honeybee. Mich. Agr. Col. Exp. Sta. Tech. Bull. 34, pp. 1–28.

SHARP, DALLAS LORE. 1925. The Spirit of the Hive. pp. 1–240.

SHUCK, S. A. 1882. Mating of a queen bee. Amer. Bee Jour., v. 18, p. 789.

SINNOTT, E. W., and DUNN, L. C. 1925. Principles of Genetics. pp. 1–431.

SLADEN, F. W. L. 1916. Bees and how to keep them. Dom. of Can. Dept. Agr. Bull. 26, pp. 1–56.

———. 1920. The Sladen two-queen system. Amer. Bee Jour., v. 60, pp. 84–86.

SMITH, JAY. 1923. Queen Rearing Simplified. pp. 1–119.

STURGES, A. M. 1924. Practical Beekeeping. pp. 1–308.

SNODGRASS, R. E. 1910. The anatomy of the honey bee. U. S. Bur. Ent. Tech. series, No. 18, pp. 1–162.

———. 1925. Anatomy and Physiology of the Honeybee. pp. 1–327.

SWAMMERDAM, J. 1735. Biblia naturae. Eng. transl. from Dutch and Latin by Thos. Flloyd, 1758, pp. 159–236.

SYLVIAC. 1902. Guide pratique de l'apiculteur amateur. pp. 1–615.

VIRGIL. 30 B.C. The Georgicks of. Transl. by J. Martyn, 1740. Book 4, pp. 341–421.

VON BUTTEL-REEPEN, H. 1907. Are Bees Reflex Machines? transl. by Mary H. Geisler. pp. 1–48.

WATSON, L. R. 1927. Controlled Mating of Queen-bees. pp. 1–50.

———. 1927. Controlled mating of honeybees. Amer. Bee Jour., v. 67, pp. 235–236. pp. 300–302. pp. 364–365.

WHITING, P. W. 1918. Sex determination and biology of the parasitic wasp, *Hadrobracon brevicornis*. Biol. Bull., v. 34, No. 4, pp. 250–256.

———. 1921. Heredity in wasps. Jour. of Heredity, v. 12, No. 6, pp. 262–266.

———. 1921. Studies on the parasitic wasp, *Hadrobracon brevicornis*. Biol. Bull., v. 41, No. 3, pp. 153–155.

———. 1923. The analysis of genetic differences through haploid parthenogenesis. Eugenics, Genetics and the Family, v. 1, pp. 102–105.

———. 1922. Heredity in the honeybee. Jour. of Heredity, v. 13, No. 1, pp. 1–8.

WHITING, ANNA R. 1925. The inheritance of sterility and of other defects induced by abnormal fertilization in the parasitic wasp, *Hadrobracon juglandis*. Genetics, v. 10, pp. 35–58.

WRIGHT, SEWELL, 1920. Principles of livestock breeding. U. S. Dept. Agr. Bull. 905, pp. 1–67.

ZANDER, ENOCH. 1910. Die Gliederung des thoracalen Hautskelettes der Bienen und Wespen. Zeit. wiss. Zool., v. 95, pp. 507–517.

EXPERIMENTS ON LONGEVITY

By RAYMOND PEARL

Institute for Biological Research, The Johns Hopkins University

(The substance of this paper was presented as a lecture, on the Schiff Foundation at Cornell University, May 9, 1928)

THE PROBLEM

THERE is something fascinating in the idea of experimenting with longevity. The span of life is a rude and uncompromising inhibitor and limiter in human affairs. Just about the time that a man's experience in living has attained a sufficient magnitude to give him some confidence that he has acquired a little skill in that difficult art, Death comes stalking along and ends it all. Furthermore death, coldly and unfiguratively considered merely as a biological process, has the unfortunate characteristic of irreversibility. So any experimental approach to its study, with man in the traditional guinea-pig rôle, is not feasible.

In the face of such a situation there are two things which the person curious about death, longevity, and similar subjects may do. He may either content himself with the monotonous *pabulum* of human vital statistics—not entirely innutritious, to be sure, but still a diet so narrowly constructed, so lacking in savor, and so full of indigestible residues that it has a tendency to induce in those who nourish themselves exclusively upon it a certain bilious and acidulous temperament, a leptosomal *habitus* of body, and mental delusions of righteous exactitude as irritating as they are unwarranted.

Or, on the other hand, the inquisitive person whose dilemma we are endeavoring to resolve, may study mortality and longevity experimentally, in some organism other than man. This means that he can subject his animals to all sorts of influences, completely under his control, and see how their duration of life is affected. Out of all this are likely to come many thrillingly unexpected things. On account of the general happiness and good cheer thus engendered there is induced a tendency towards a pyknic or eurysomal *habitus* of body, and a tolerant realization of the liability of human beings to draw erroneous conclusions from what seem—but unfortunately too often *only* seem—to be plain facts of nature. There is sound tradition for such an effect. The Greeks, the Chinese, and the Hindus all represented their gods as of a pyknic habit, and, as everyone knows, the chief activity of gods is to make biological experiments with human beings.

Not wishing to miss any of the pleasures of life, I have myself tried both the statistical and the experimental methods of studying mortality and longevity. But tonight I shall speak to you only about the results reached by the latter method. In short our discourse is to be about such lowly organisms as flies and muskmelons, and has nothing whatever to do with man directly. Perhaps the

general biological principles which we shall find operating in these lower forms relative to longevity also apply, in some degree, to the determination of the human life span, but I am not prepared positively to assert that this is so in this particular case. There seems to me to be some probability that it is so, but how great this probability is cannot be precisely evaluated in the present state of knowledge. I have confidence, however, in the general biological principle recently stated by J. B. S. Haldane in these words: "Whatever additional facts may be true of humanity, it is subject to the same laws as those which govern the animals from which it has arisen."

LIFE TABLES

The simplest experiment that can be performed about longevity is to take a considerable number of individual organisms, say a thousand fruit flies (*Drosophila*), at the moment of birth (which we shall for convenience in the case of *Drosophila* take as the moment of emergence as imago from the pupa case), confine them in suitable receptacles for

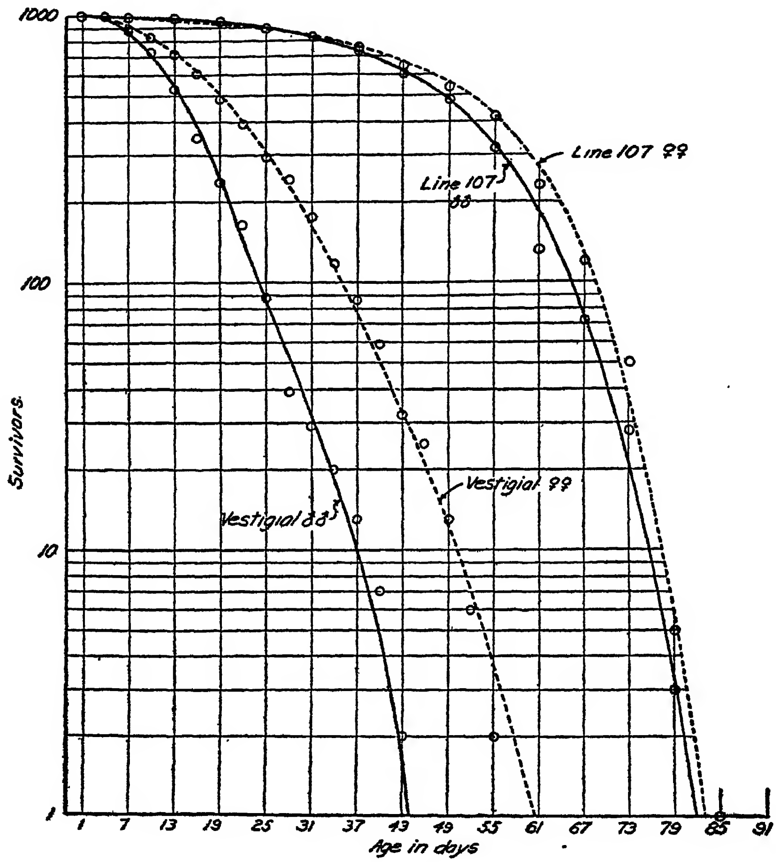


FIG. 1. SHOWING THE NUMBER OF FRUIT FLIES SURVIVING AT DIFFERENT AGES, OUT OF 1000 STARTING IMAGINAL LIFE TOGETHER

The upper pair of lines relate to the normal wild type *Drosophila*, and the lower pair to the mutant *vestigial*

observation, feed and care for them properly, and observe the times at which the individuals die, until the last one of the thousand has ceased to live.

The result of such an experiment is shown in figure 1.

These curves bring out several important points regarding the duration of life in flies. The first is that there are differences between individuals in respect of longevity. Under identical conditions of environment, housing, feeding, etc., some individuals live longer than others, and the distribution of these differences in longevity is a regular and characteristic one. In the second place, if we compare the upper two lines of the diagram, which depict the facts for normal, wild type *Drosophila*, with the lower two lines, which relate to the mutant form vestigial, characterized by greatly reduced and distorted wings, it is seen that these two different races or strains of flies have, as races, characteristically different average durations of life and different distributions of longevity under standard laboratory conditions. Vestigial flies live, under the same environmental conditions, only about a third as long as normal wild type flies, on the average. Finally the diagram shows that female flies live longer than males, on the average.

The facts shown in figure 1 are descriptive of the distribution of longevity in populations of flies of two sorts, wild and vestigial. But, like all descriptions of natural phenomena, their primary effect on the inquiring mind is that they definitely formulate problems. What we want to know is why it is that some individual flies live longer than others, and that some kinds of flies (normal wilds) live longer than other kinds (vestigials). When we say "why" in this connection, what we really mean, of course, is that we want to know what are the variables which are causally determinative of the observed facts. Let us now see what can be found out in this direction.

INHERITANCE OF LIFE DURATION

The first question which occurs to the biologist when confronted with any such problem is naturally as to what heredity has to do with the results. Light upon this query may be got in two different ways. We may first try to determine whether differences in longevity between individuals of the same strain and in the same population have a genetic basis.

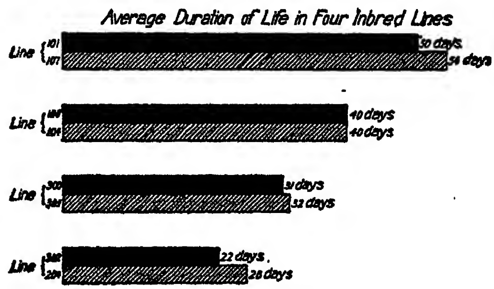


Fig. 2. Showing the Mean Duration of Life, in Days, of Four Inbred Lines of Drosophila, All Isolated Originally from the Same General Population

The solid bars show the duration of life in the line at its first test, and the cross-hatched bars the duration of life in the same line tested about seven months later.

One way of doing this, which is standard in genetic methodology, is to form inbred lines through the process of successive brother × sister matings, and then see whether significant differences in longevity are permanently characteristic of different inbred lines so produced. The result of such experiments on duration of life in *Drosophila* is to show that, in fact, inbred lines or strains showing permanent differences in longevity can be produced by isolating and propagating in this way individuals from a general mixed population which, in current genetic terminology, is not homozygous relative to the

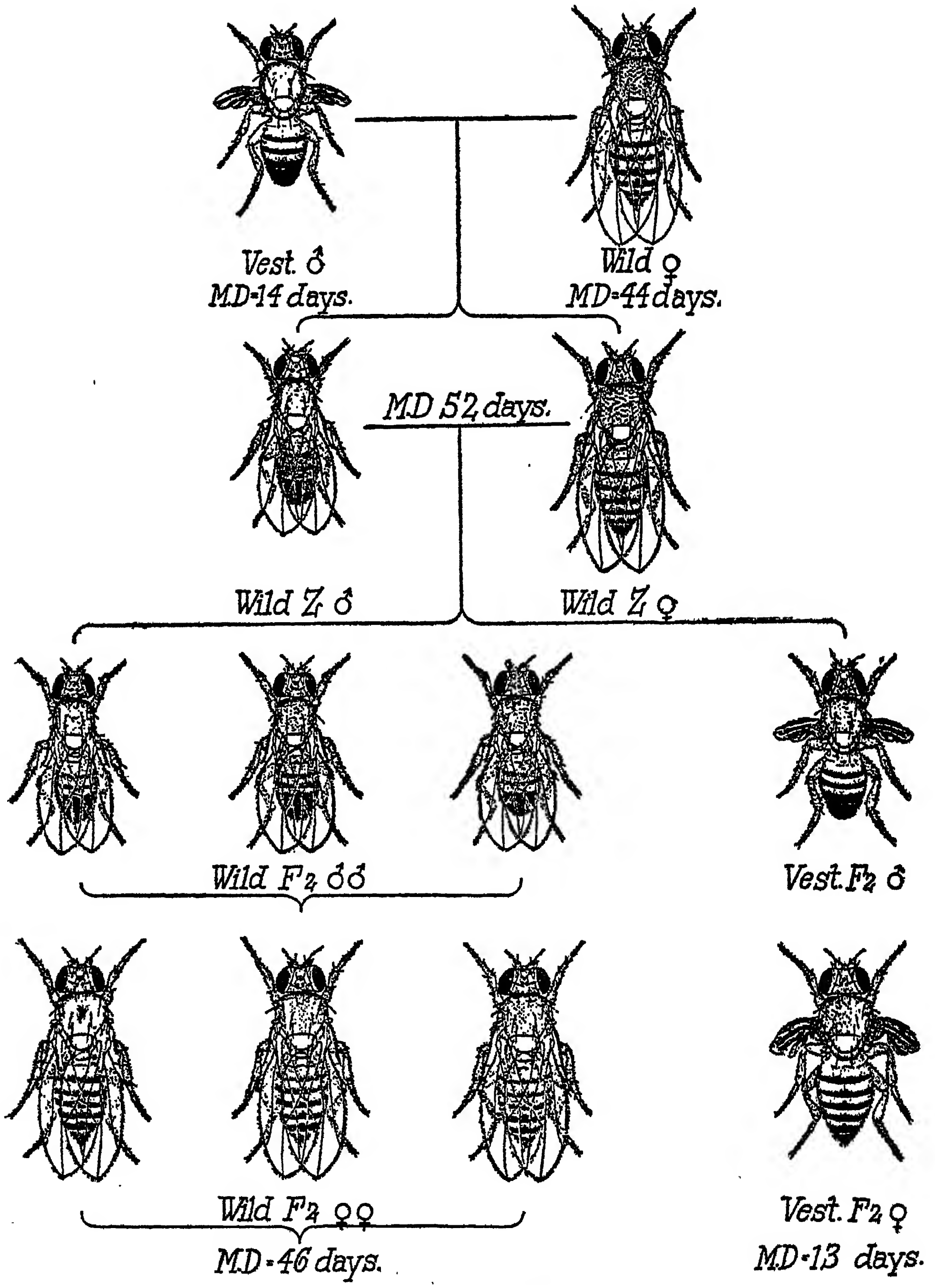


FIG. 3. PEDIGREE DIAGRAM SHOWING THE RESULTS IN THE FIRST TWO GENERATIONS OF CROSSING A VESTIGIAL MUTANT WITH A NORMAL WILD DROSOPHILA

genetic factors which may be presumed to determine longevity. Examples of this are shown in figure 2.

This diagram demonstrates conclusively that there exist in a general population of *Drosophila* large differences in longevity which can be made permanent by breeding. As a matter of fact some of these lines are still carried as stocks in the laboratory, and have preserved substantially unchanged the average duration of life shown in figure 2 for eight years, without further selection, or brother × sister mating.

Another kind of evidence demonstrating the inheritance of longevity in *Drosophila*, under constant and defined environmental conditions, can be obtained by crossing a long-lived strain with a short-lived strain, and analyzing the results in successive generations of progeny in the usual Mendelian manner. Such crosses were first made between normal wild type flies and the mutant vestigial. Figure 1 shows that these two kinds of flies have markedly different average durations of life and different life curves.

The chief, broad results of such a crossing experiment are shown in figure 3.

When flies carrying the mutation vestigial are crossed with normal, wild type flies, the wing mutant character vestigial behaves as a simple Mendelian recessive, without sex-linkage, since the gene for vestigial is located in the second chromosome. The first generation flies from such a cross are all of the normal wild type, with normal wings. When these first generation flies are mated with each other, they produce a second generation in which individuals bearing normal wings and individuals bearing vestigial wings occur in the theoretical proportion of three of the former to one of the latter. The actually realized proportions approximate to this theoretical ratio.

In respect of duration of life the facts are these. The vestigial strain used as parent in the cross had an average duration of life of approximately 14 days. The wild type strain used as the other parent had an average longevity of 44 days. In the first generation flies, which are all of normal wild type morphologically, the mean duration of life was approximately 52 days. When these first generation flies were bred with each other the wild type flies of the second generation had a mean duration of life of 46 days, while the recessive vestigial flies of this second generation had a mean duration of life of only 13 days. There thus appears a clean segregation in respect of average longevity exactly paralleling that in the morphology of the wings. The forms segregated in the second hybrid generation have the same average duration of life as the corresponding original parent forms, to within one or two days.

A great many experiments of this type have been carried out in my laboratory, involving a number of mutations other than vestigial. What they all show clearly is that duration of life behaves like a segregating character in the Mendelian sense. How are these facts to be interpreted?

The most reasonable interpretation, consonant with all the facts, seems to be to assume that duration of life, considered of itself, is not a biologically separate characteristic of the organism, but instead is simply the expression of the total functional-structural organization or pattern of the individual. It is apparently this organization or pattern which is inherited, and not duration of life as such. Duration of life is only one of many objective manifestations of the thing which is inherited. Put in another way, what this view of the matter says is that if the duration of an individual's life is an implicit function of the individual's or-

ganization or constitution (presumably a purely physical and chemical thing fundamentally) and if constitution or organization is inherited, it follows that duration of life will behave exactly as though it were itself inherited.

In the experiments here described it would seem that the gene for vestigial, besides affecting the form, size and behavior of the wings of *Drosophila*, *also* influences in and through its effects on the total organization pattern of every fly in which it is present, the duration of life of that fly. We have measured with considerable exactness and manifoldness what the quantitative effect of this gene is upon duration of life (and, of course, at the same time the effect of its allelomorph, the gene for normal wing), under standard and constant laboratory conditions of feeding, etc.

The view of the case which has been sketched seems to be in accord with the best current opinion as to the biological meaning and effect of mutant genes generally.

DENSITY OF POPULATION AND LONGEVITY

Shall we regard the matter as now settled, and conclude that in the genetic constitution of the individual we have the determining cause of its longevity? Before doing so it would seem the part of wisdom to see what effect environmental changes may have upon the duration of life of *Drosophila*. We have made many studies in this direction, but within the present time limitations it will be possible to discuss only one environmental factor. This one is the density of population in the universe wherein the individual lives its life; or, to put the case in less technical terminology, the degree of crowding to which the individual fly is subjected by its fellows.

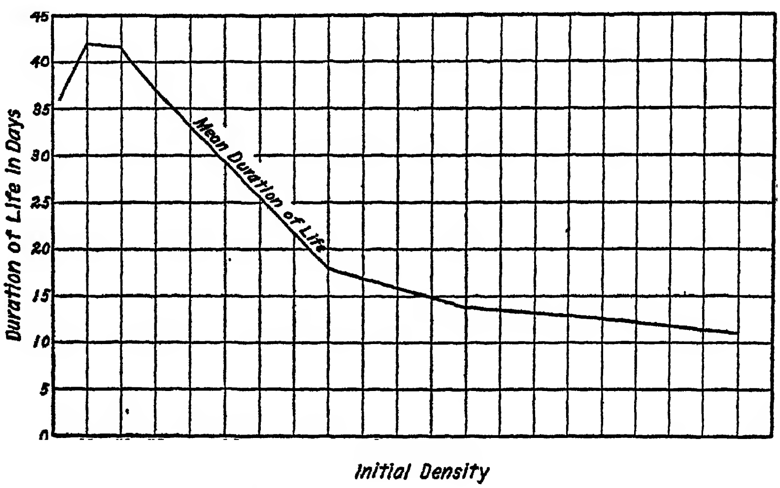


Fig. 4. Mean Duration of Life of Wild Type Drosophila at Different Densities of Population

The story of the effect of density of population upon longevity is such a long and complicated one that it will be impossible here to do more than touch briefly upon its high points. If one makes up a series of one-ounce vials each containing newly hatched flies, in numbers varying from one or two pairs per bottle

up to say 500 flies, and then determines the time of death of each fly in each bottle, it is found that the average duration of life follows, with increasing density, the course shown in figure 4.

Between initial densities of 2 and 15 flies per ounce bottle the mean duration of life increases rapidly with increased density. Between densities of 15 and 55 flies per bottle there is a slow and gradual increase in average longevity. In fact it is not certain that this region of the curve does not really represent a plateau of optimal density, in which region small differences in density have no great effect upon average duration of life. After a density of 55 flies per bottle is passed longevity declines steadily with advancing density.

The form of the upper limb of the curve of decreasing average longevity with increasing density of population suggests that there is a tendency to approach a constant level at extremely high densities. There is only a very gradual decline of mean duration of life with increasing densities of population after a density of 200 flies per bottle has been passed. Beyond this density little further effect on longevity is produced by greater crowding.

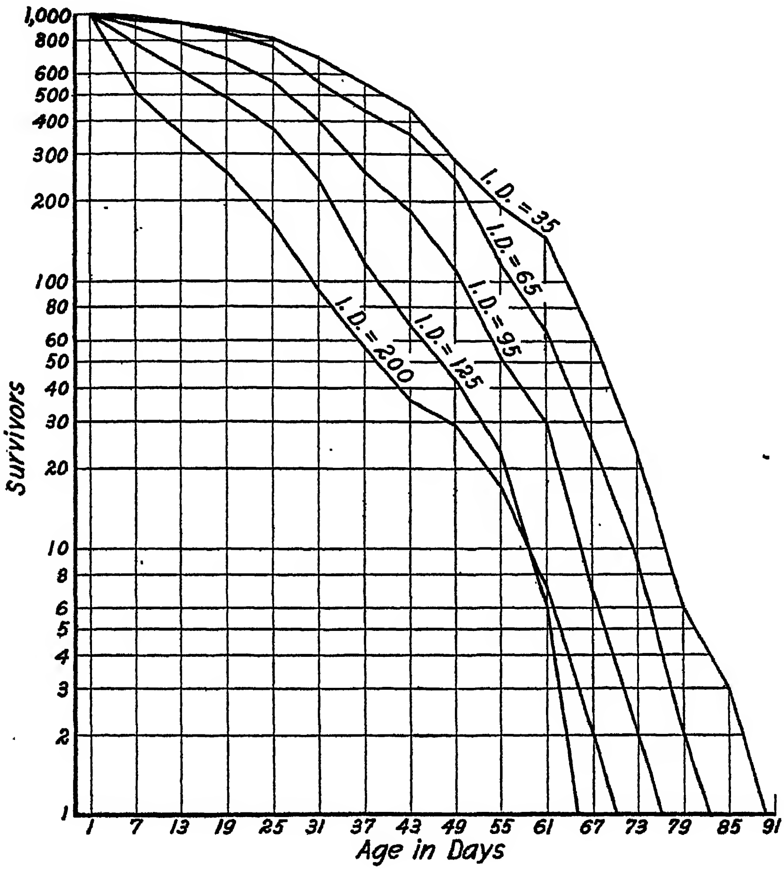


Fig. 5. Survivorship Distributions for Initial Densities of 35, 65, 95, 125, and 200 Wild Type Flies per Bottle

If we examine the curves of survivorship at different densities of population certain further points of importance are apparent. In figure 5 are shown survivorship curves at the optimal density of 35 flies per bottle, and at five higher densities.

From figure 5 it is seen that at density 200, not only has the mean duration of life of the normal wild type flies been greatly reduced, but also the survivorship curve for such flies has been transformed into something practically identical with the straight line diagonal type of life curve shown in figure 1 to be characteristic of the mutant fly vestigial.

So then we find ourselves in a somewhat paradoxical situation. One body of experimental evidence seems to show clearly that differences in life duration and in the form of the life curve have their foundation in the genetic constitutions of the individuals—in heredity, in short—whereas another body of equally careful and cogent evidence indicates that by appropriate modification of the environment (density of population) it is possible to alter the mean duration of life and the form of the life curve of long-lived wild type *Drosophila* to a point where these characteristics become substantially identical with those normally found in the short-lived mutant form vestigial.

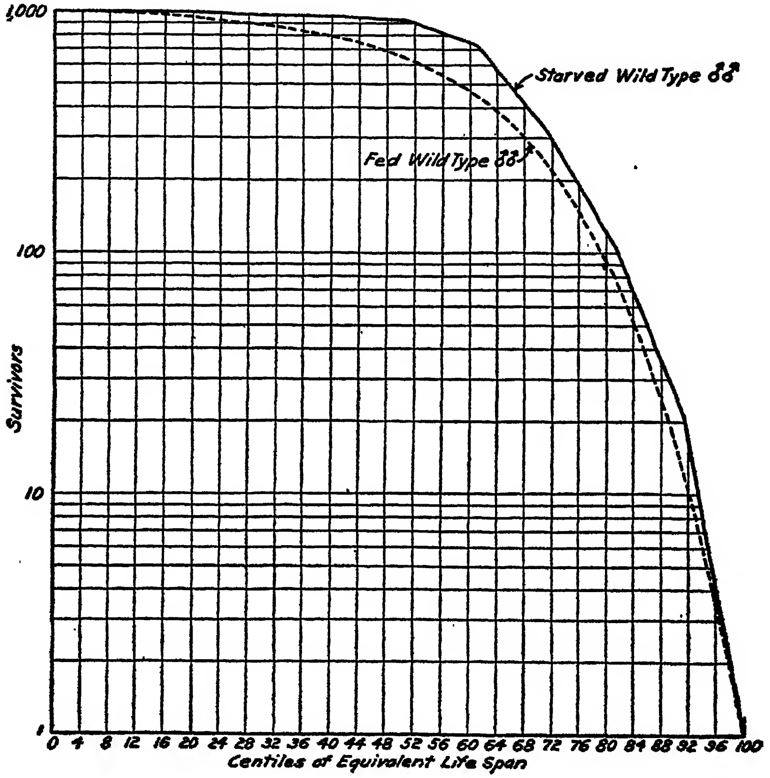


FIG. 6. COMPARING THE SURVIVORSHIP CURVES ON A CENTILE AGE BASIS OF (*a*) STARVED WILD TYPE MALES (SOLID LINE) AND (*b*) FED WILD TYPE MALES (BROKEN LINE)

Plainly further, and more penetrating, analysis of the situation is demanded. In order to accomplish this attention may next be turned to a different line of experi-

mental approach. Experiments were carried out, with the most painstaking attention to details of technique, in order to secure reliability of results, in which flies were hatched under such conditions that, fed flies. Two general results of significance emerged from these experiments. The first is shown in figure 6, and the second in figure 7.

In making this diagram, shown in

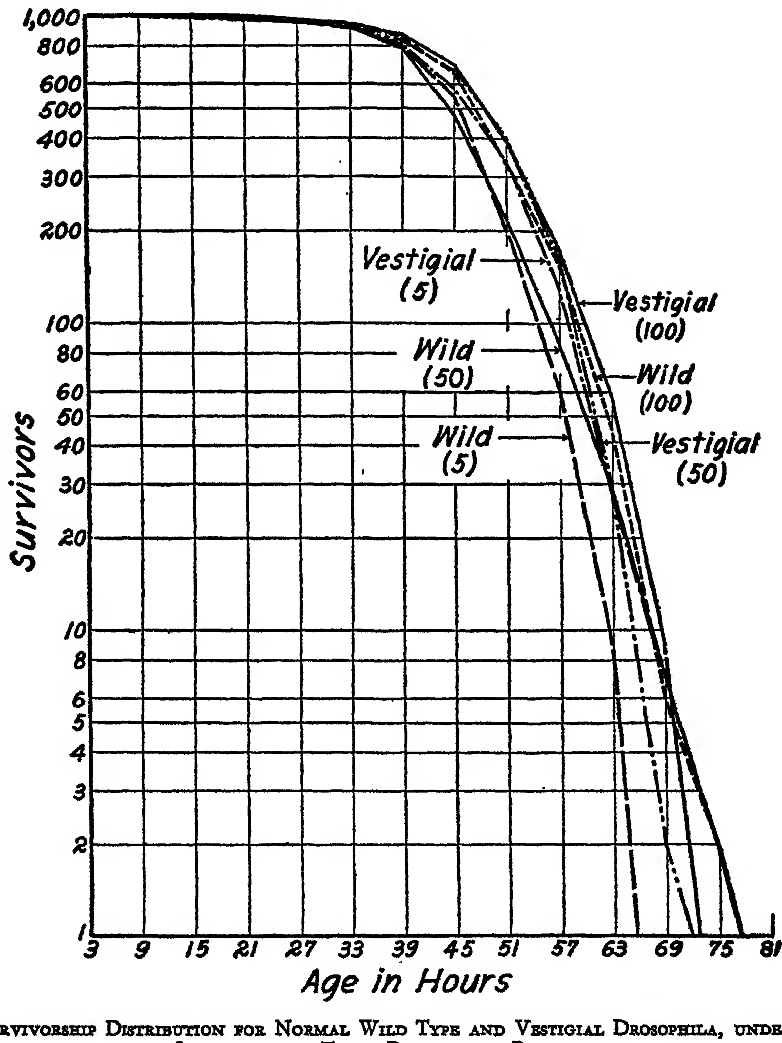


FIG. 7. SURVIVORSHIP DISTRIBUTION FOR NORMAL WILD TYPE AND VESTIGIAL DROSOPHILA, UNDER COMPLETE STARVATION AT THREE DENSITIES OF POPULATION

as fully developed flies, they could never obtain any food. Under the conditions of complete starvation the durations of life of large numbers of individuals were observed. These durations were a matter of hours, instead of days as in the normally figure 6, it was necessary, in order to compare the forms of the life curves of fed and starved flies, to measure age in relative terms, instead of absolutely in hours or days. This was done by taking the total life span as 100 per cent of life duration,

in the case of both fed and starved flies. Then age may be expressed in both cases as hundredths, or centiles, of their own life span in the case of each group of flies. When this is done, with the result shown in figure 6, it is seen at once that while complete starvation reduces the absolute average length of life from about 45 days to about 45 hours, the *form*, or shape, of the survivorship curve remains *unaltered*.

In carrying out these experiments different densities of population were used. This circumstance led to the second significant result, which is shown graphically in figure 7.

The net result of these experiments is evident from the diagram. Under conditions of complete starvation different densities of population, over the range from 5 to 100 inclusive, produce no significant effect whatever upon duration of life. The mean duration of life in hours is approximately the same, about 44 hours for male flies, and roughly 10 per cent higher for female flies, *at all densities*, and for both wild type and vestigial flies.

INHERENT VITALITY

From the point of view of theoretical biology the condition of complete starvation is an interesting one. It means that we are observing the physiological behavior of the organism in pure form, so to speak. This is evident from the following adaptation of Cuvier's old "whirlpool"* conception of the organism.

$A \longrightarrow$	$B \longrightarrow$	C
External Sources of Energy and Non-Living Matter	*The Organism*	*The Product*
(Food. Either chemical compounds of external origin which yield energy and utilizable material when split by the organism (animals), or similar compounds synthesized by the organism itself, with energy derived from light, and subsequently split to yield energy and utilizable material.)	(An aggregation of matter which has the property of autonomously changing A to C, *by virtue of its pattern or organization.*)	(Either (*a*) heat, (*b*) work, (*c*) component matter of the organism, or (*d*) waste, meaning chemical compounds incapable of yielding energy with economic profit by further splitting.)

The concept of the organism embodied in this scheme is, of course, an old one. Lately Pikler has discussed a similar but more detailed and complete outline of the relation of organism and environment.

What the organism does under experimental conditions such that we can observe B of the above scheme free from the disturbing influence of A, I have chosen to call expressions of *inherent vitality*. Inherent vitality may be precisely defined as *the total potential capacity of an organism to perform vital actions, in the complete absence of exogenous derivation of matter or energy*. From the standpoint of energetics solely it is analogous to the potential energy of a charged Leyden jar. This concept has nothing whatever to do with vitalism, but is, on the contrary, purely mechanistic.

The results depicted in figure 7 show that the difference between normal wild type flies and vestigial flies in respect of duration of life, which under normal conditions of feeding (that is, when it is the expression of the total vitality implicit in the normal $A + B$ physiological economy) follows the Mendelian law of inheritance, is *not* dependent upon a fundamental difference between these two kinds of flies in *inherent* vitality. This difference, on the contrary, appears merely to be due to the fact that under the environ-

mental conditions represented by the standard fly husbandry of the laboratory (the *A* of our schema) vestigial flies were not able to bring their inherent vitality to so complete expression in duration of life as were the wild type flies under the same conditions.

This result is a specific example of the general principle that the somatic expression of any genetic factor in any particular case is in part a function of the general environmental situation which exists in that case. It has been demonstrated that *under the standard feeding conditions for laboratory bred Drosophila* the gene for vestigial has as a part of its somatic expression a considerably reduced duration of life as compared with the wild type. There are few cleaner-cut examples of Mendelian segregation to be found in the whole literature of genetics than that of *Drosophila* with respect to longevity. Yet the results just described show that the whole of that part of the somatic expression of the vestigial gene which is differential in respect of duration of life disappears under another system of "feeding" wild type and vestigial flies (namely, complete starvation).

An example, from quite a different field, of the general principle that environmental conditions must be optimal for the expression of the character, if reliable genetic conclusions are to be drawn, is afforded by the recent work of Hoffer, who showed that selfed lines of maize made better growth when grown in clay soils, whereas hybrids of the same lines grew better in loam soils.

SEEDLING GROWTH AND LONGEVITY

The manifestations of inherent vitality can be studied in plants even more favorably than in animals. The dry seed of a dicotyledonous plant, like a canteloupe (*Cucumis melo*) let us say, is a complete but undeveloped individual. It contains in the cotyledons, which are morphologically leaves of the preformed plant which the seed includes, stored nutritive material sufficient to carry the seedling on until the nutrition can be obtained by absorption through the roots and by photosynthesis. The cotyledons, and the stored nutriment which they contain, are an integral part, and a very important part, of the total organic pattern of the individual. If now we sterilize such a seed, plant it on a medium which contains no food material upon which the roots can draw, and keep the whole preparation in the dark, the growth of the etiolated seedling which ensues is an expression of the *inherent vitality* (as defined above) of that individual. The seedling must draw whatever nutriment it gets from endogenous sources, which are themselves an integral part of the total organized pattern of the individual. Again we shall be able to discuss the *B* element of our scheme, the organization of the individual, freed from the disturbing influences of *A*.

Now suppose we set up an experiment of the following sort. Long glass tubes, closed at one end like a test tube, are made by the glass blower. In each of these tubes is poured 40 cc. of a 2.5 per cent solution of agar in distilled water. The agar has been purified by repeated washing in distilled water, until all soluble material has been removed from it. The tubes and their contents are then sterilized in an autoclave. After the agar has cooled and set to a jelly there is placed on its surface, with aseptic precautions, one canteloupe seed, which has been specially prepared in the following way. In the first place all the seeds for a given experiment are the produce of a single melon grown the year before in our experimental garden. In this way approximate genetic homogeneity in the ex-

periments is secured. Each seed is individually weighed and measured and the selection of the seeds to be used based upon these quantitative data. Then, under aseptic precautions, the testa is removed from each selected seed. The shelled seeds are then sterilized by immersion for one minute, with stirring, in a 1:1000 bichloride of mercury solution, following by rinsing in sterile, distilled water. The seeds are then soaked for three hours in sterile distilled water, in such a way as to ensure that each seed is not in contact with any other, and that therefore all have an equal chance to absorb water. After soaking, one seed is carefully placed on the top of the agar in each tube. The tube is then tightly sealed with a sterile cork or with sterile cotton. The tubes are placed in light-tight boxes and put in an electric incubator running at 30°C.

What happens in such an experiment is shown schematically in figure 8. In this diagram the horizontal scale represents time and the vertical scale the size of the seedling plant.

There is first the *period of growth*. During this period the seedling is actively growing. A richly branched root system develops in the agar substrate. Above it rises a straight unbranched stem, bearing the cotyledons at its top.

The period of growth is followed by the *period of suspended animation*. After growth has ended the seedling remains without visible change for a varying number of days, not growing but still living, with cells in full turgor, and in every way entirely normal in appearance. The plant is living and carrying on metabolism, but it has stopped growing.

The period of suspended animation is followed by the *period of death*. A time comes when the seedling begins to die. Death is a progressive process which requires a number of days to complete. The gradual progressive nature of the death of the seedling makes a practical trouble in the experiments. It is difficult to decide upon and to read an end-point of total duration of life. The series of events involved in the death of the plant are nowhere sharply and precisely delimited. The stages grade into each other by a gradual continuous process difficult to break up observationally into discontinuous phases, for the simple reason that

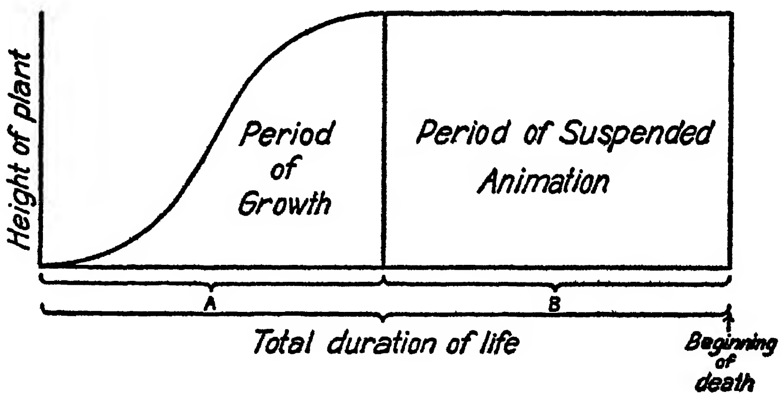


Fig. 8. Diagram to Show the Course of Events in an Experiment on Inherent Vitality with Canteloup Seeds as Material

death *is* fundamentally and inherently continuous from the time that breakdown starts until the last cell is dead.

We have studied various "end-points," and have found the most reliable and least variable, because capable of being read with the greatest certainty, to be the beginning of death, as evidenced by the first appearance of abnormality of the stem, in the continuous series which invariably ends finally in the complete death of the seedling.

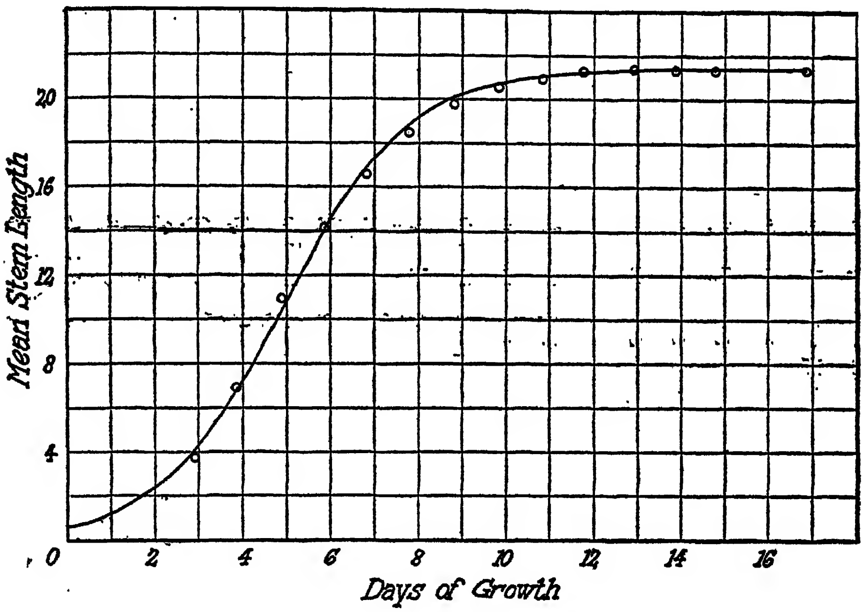


Fig. 9. Observed (Circles) and Calculated (Smooth Curve) Mean Stem Length of Canteloup Seedlings Grown in the Complete Absence of Exogenous Food and Light

In such an experiment the seedling grows in length in close correspondence to a logistic or autocatalytic curve. This curve has been found widely useful in describing the course of growth in both individuals and populations. How closely the actual experimental results with the canteloupe seedlings, under conditions of inherent vitality, follow the logistic curve, is shown graphically in figure 9.

The time duration of both the growth period and the period of suspended animation, and therefore by necessary consequence the total duration of life, varies considerably from individual to individual. Now if we determine the correlation between the rate of growth during the growing period (that is, the increase in stem length of the seedling per unit of time), on the one hand; and the total duration of life to the beginning of death, on the other hand, the correlation comes out to about −0.5 or −0.6. This is a substantial correlation. It demonstrates that there is a significant association between individual differences in rate of growth on the one hand and duration of life on the other hand, in this group of seedlings, grown under such conditions that both of these phenomena are necessarily dependent solely upon the inherent vitality of the individual as here defined.

There can be no reasonable doubt as to the correctness of the conclusion that con-

sistent and accordant results will be obtained if inherent vitality, the manifestations of which are dynamic expressions of the biological organization of the individual, be measured by observation either of growth or of duration of life.

The negative sign of the correlation between growth rate during the growth period and total duration of life means that the faster the rate of growth the shorter the duration of life, and *vice versa*. This result confirms experimentally the point of view expressed some years ago in my book *The Biology of Death*, where it was suggested that duration of life depends fundamentally upon two variables:

a. The constitution (organization or pattern) of the individual, genetically determined.

b. The average rate of metabolism or rate of energy expenditure during life.

On this view, if the average rate of metabolism, or of energy expenditure, is high the duration of life will tend to be shortened, while if, for any reason, the average metabolic rate or rate of energy expenditure is low the total duration of life will tend to be prolonged.

Entirely independent experimental confirmation of this result is furnished by the work of MacArthur and Baillie on the mortality of *Daphnia magna*. They find that

The relative longevity of the sexes may be expressed as varying inversely with their average rates of metabolic activity. The average age at death for males was 37.8 and for females 43.53 days, the duration of life for females exceeding that for males by 14.6 per cent. Now in metabolism, as estimated by heart rate, the males surpass the females by nearly the same percentage, and the product: heart beats per second (weighted average through life) × average age in days at death = a constant, *e.g.*

Males: 4.3 beats × 37.8 days = 161.54
Females: 3.7 beats × 43.8 days = 162.06

The experimental data thus tend to support the view that a definite endowment of vital energy, potential in the protoplasm of the species and line, may be transformed and expended rapidly, as in the short-lived males, or more slowly, as in the longer-lived females. The evidence so far available indicates also that length of life in *Daphnia magna* has the usual temperature coefficient for a chemical reaction. Other factors being equal, it would seem that, at least in this species, longevity is a function of metabolic rate.

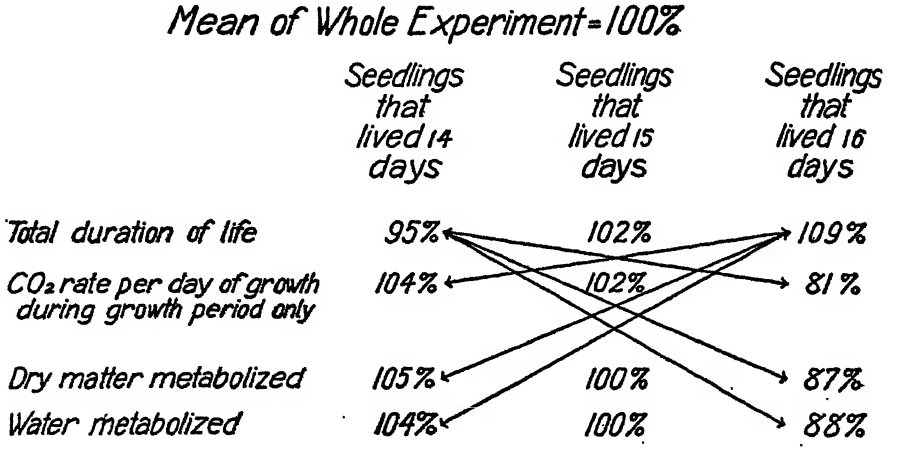


FIG. 10. CHART SHOWING RESULTS OF SEEDLING METABOLISM EXPERIMENT

SEEDLING METABOLISM

During the past year we have been carrying on some experiments with cante-

loupe seedlings, which still further confirm and extend our results. To the experimental situation which has been described above, there has been added the determination of the carbon dioxide produced by the respiration of the seedling throughout each period of the experiment, and also determinations of the total metabolic transfer of dry matter from the cotyledons to the stem and roots, and of water from the purified agar substrate to the seedlings. I shall not weary you with a description of the elaborate technique required to measure accurately the respiration of a single cantaloupe seedling growing in the dark. The plant physiologists present know all about the tribulations incident to such endeavors. The rest of you would be bored with their recital. The details must be reserved for publication in a technical journal, but I wish to present here, for the first time, in a preliminary way, some results of one experimental run, which involved 7 seedlings. Of these 7 seedlings 3 lived, to the beginning of death, 14 days; 3 lived 15 days; and one, 16 days. If we express the average condition of each variable for the whole group in this experiment as 100 per cent we then have the results shown in figure 10.

The number of seedlings involved in this experiment is far too small to have anything but suggestive value, taken by themselves. But a great deal more work has been done along the same lines, always with the same results in principle, which will in due time be published in full detail. This particular experimental run is taken for illustration simply for the reason that it was the first definitive experiment in which the hypothesis developed above as to inherent vitality and duration of life was tested biochemically.

The general upshot of all this work is that those seedlings which have a relatively rapid rate of CO_2 production in respiration during the growing period, and which metabolize a relatively large amount of dry matter and of water during growth, live a shorter time in total than do seedlings which have a relatively slow CO_2 rate, and a relatively small metabolic transfer of dry matter and water, during growth. The relatively long-lived plants lived at a slower rate than the relatively short-lived plants. In figure 10 lines are inserted connecting relative duration of life with approximately equal relative metabolic rates. These lines run across the diagram.

SUMMARY

Let us now bring together in summarized form the results of the different lines of experimentation that have been briefly described in this lecture. Starting with the fruit fly *Drosophila melanogaster* and its mutant form called vestigial, we have seen that the normal wild type of fly dies according to a characteristic, normal sort of life curve. But under the same experimental—that is to say, in this case, environmental—conditions the vestigial mutant form has a quite different life curve, not only in respect of absolute average duration of life, which is only about one-third that of the wild type fly, but also in the whole shape of the curve.

Under these conditions of identical environment these differences between wild and vestigial flies behave in inheritance exactly like a simple Mendelian character, when the two kinds of flies are bred together.

At the same time, however, by modifying one element of the environment, the density of population or degree of crowding, it is possible to convert the normal wild type curve over into the vestigial life curve.

This apparent paradox makes it neces-

sary to probe deeper into the matter, which has been done by devising experiments of such a character that we are enabled to study the organization, the constitutional make-up or pattern, of the organism free from the disturbing influence of the necessity normally present in biological work for the organism to derive its energy from sources external to itself. When this is done it at once appears that the apparent genetic difference between wild and vestigial *Drosophila* in respect of duration of life, which so clearly manifests itself in Mendelian experiments, is really only a result of the fact that in a normal environment, optimal for wild type flies in respect of food, vestigial flies are not able to bring to complete somatic expression their inherent potential viability. Vestigial and wild type flies are seen, under these conditions, to have the same inherent vitality. Furthermore, under these conditions, altering the density of population does not alter the shape of the life curve or the average absolute longevity.

With the confusing effects of the interrelationship of heredity and environment thus experimentally cleared away, we are able to plan experiments which will give us some real insight into the basic biological variables which determine longevity. And parenthetically it may be remarked that in a great deal of standard genetic work with what may be loosely called "physiological" in distinction from "morphological" characters, there perhaps inheres the same kind of confusing interrelationship in the effects of heredity and environment which led to the initial paradox in the fly work we have discussed. There is an underlying postulate, usually unrecognized and almost never discussed, implicit in nearly all genetic work. It is that, if in a constant environment A, a difference between two organisms such that one has the character in the condition B and the other in the condition B', segregates in the second filial generation following a cross, the difference between B and B' is to be regarded as genetically determined or caused. But this postulate is only completely valid if it has first been demonstrated that the environmental condition A is equally favorable for the development to complete somatic expression of *both* B and B'.

To come back now to our own trail, it has been possible to show, by experiments with cantaloupe seedlings so devised that we are working solely with inherent vitality, that the duration of life or longevity of the individual varies inversely as the rate of energy expenditure in metabolism during life. In short, the faster an organism lives, the sooner it dies.

This, then, is the conclusion at this stage of a continuing program of experimental research on the biology of life duration or longevity. This conclusion may, and doubtless will, be modified, refined, and extended as the experimental program continues, but I think it is hardly likely to be reversed.

LIST OF LITERATURE

Note: Inasmuch as there is an extensive bibliography on the subject of this paper in the author's recent book *The Rate of Living. Being an Account of Some Experimental Studies on the Biology of Life Duration*, New York (Alfred A. Knopf), 1928. Pp. 185; and London (University of London Press), 1928, it seems unnecessary to do more here than to list a few supplementary titles beyond those covered in the work cited. These are as follows:

(1) Abrahams, A. On the physiology of violent exercise in relation to the possibility of strain. Lancet, March 3, 1928, pp. 429–435.

(2) Buxton, P. A., and G. H. E. Hopkins. Re-

searches in Polynesia and Melanesia. An Account of Investigations in Samoa, Tonga, and Ellice Group, and the New Hebrides, in 1924, 1925. Parts I–IV (Relating principally to Medical Entomology). London (London School of Hygiene and Tropical Medicine), 1927. Pp. xi + 260. Plates I–XII.

(3) Friedjung, J. K. Die hohe Kindersterblichkeit in kinderreichen Familien. Wiener Klin. Wchnschr., Jahrg. 40, pp. 1578–1579, 1927.

(4) Gould, A. The longevity of grandparents. Eugen. News, Vol. 12, pp. 166–171; 175–178, 1927.

(5) Gutherz, S. Der Partialtod in funktioneller Betrachtung. Jena (Fischer), 1926. Pp. v + 66.

(6) Hill, A. B. Cricket and its relation to the duration of life. Lancet, Oct. 29, 1927, p. 949.

(7) Hoffer, G. N. Some differences in the functioning of selfed lines of corn under varying nutritional conditions. Jour. Amer. Soc. Agron., Vol. 18, pp. 322–334, 1926.

(8) Jennings, H. S., and R. S. Lynch. Age, mortality, fertility, and individual diversities in the rotifer *Proales sordida* Gosse. I. Effect of age of the parent on characteristics of the offspring. Jour. Exp. Zool., Vol. 50, pp. 345–407, 1928.

(9) Korschelt, E., S. Hirsch, F. W. Harms, M. Hartmann, and H. Driesch. Leben, Altern, Tod. Berlin (H. Bermühler Verlag). No date (*ca.* 1927). Pp. 81.

(10) Lyon, C. J. [Trans. and Edit.] Kostychev's Plant Respiration. Authorized Edition in English with Editorial Notes. Philadelphia (Blakiston), 1927. Pp. xi + 163.

(11) MacArthur, J. W., and W. H. T. Baillie. Sex differences in mortality and metabolic activity in *Daphnia magna*. Science, Vol. 64, pp. 229–230, 1926.

(12) Metalnikov, S. Immortalité et rejeunissement dans la biologie moderne. Paris (Flammarion), 1924. Pp. 283.

(13) Pearl, R., A. A. Winsor, and J. R. Miner. The growth of seedlings of the canteloup, *Cucumis melo*, in the absence of exogenous food and light. Proc. Nat. Acad. Sci., Vol. 14, pp. 1–4, 1928.

(14) Pikler, J. J. Das subjektive (praktische) und das objektive (theoretische) Kriterium des Lebens. Zeitschr. f. Konstitutionslehre, Bd. 12, pp. 1–49, 1926.

(15) Pütter, A. Allgemeine Lebensbedingungen. *In* Handbuch der normalen und pathologischen Physiologie. Bd. I, pp. 322–406, 1927.

(16) Rahm, P. G. Ist der Lebensvorgang bei den Tieren der Moosfauna im erstarrten Zustand nur herabgesetzt oder ganz unterbrochen? Verhandl. Naturhist. Verein. Preuss. Rheinlande, Bd. 82, pp. 377–383, 1925 (1926).

CRITERIA FOR DISTINGUISHING IDENTICAL AND FRATERNAL TWINS

By TAKU KOMAI
Kyoto Imperial University, Japan

THE biological fact that there are two kinds of human twins and twinning phenomena is now universally acknowledged. No one doubts today the distinction between monozygotic or identical twins, who originate from a single fertilized ovum by a process which is apparently a kind of budding or fission in a broad sense, and dizygotic or fraternal twins, who come from two independent ova fertilized and implanted practically at the same time. A criterion for discriminating these two kinds of twins from each other with correctness would be of immense value to geneticists, pathologists and psychologists. There are in fact certain features of twins which, it has been maintained by previous workers in this field, serve this purpose.

THE CHORION AND PLACENTA

The foetal membranes, notably the chorion, and also the placenta in some cases, are often thought to give a very reliable decision as to whether the twins are monozygotic or dizygotic. If each foetus is covered by a separate chorion they are dizygotic, while if they are covered by a common chorion and provided with a common placenta, they are monozygotic. No doubt this rule holds true for a majority of cases. However, certain recent workers like Siemens (1924a, 1925, 1927) and v. Verschuer (1927) claim to have found instances which are at variance with it. Thus, some twins were born with separate chorions, and nevertheless show very close similarity in many physical features, while other twins very different from each other in several characteristics were covered with a common chorion at birth.

Moreover, statistical data, according to these authors, suggest the existence of such exceptional twins. There is a simple method of calculating the approximate number of monozygotic twins among a given twin population, from the number of different-sex twins found in it, which is called Weinberg's differential method. This method is based on the assumption that the sex of one of the dizygotic twins is determined independently of the other; if this is the case, there must be about the same number of dizygotic twins among the same-sex twins as there are different-sex twins, and the rest of the same-sex twins are monozygotic. By this method, the percentage of monozygotic twins has been estimated at from 26 to 36 (according to v. Verschuer's figure); this exceeds more or less the percentage of monochorionic twin-births, which is 14 to 26. It is thus likely that a small percentage of monozygotic twins are born with separate chorions.

Dahlberg (1926) criticizes the above contention of Siemens and states that the abnormal cases mentioned by the latter

author are probably due to some mistake in the diagnosis of the chorion; and moreover, as he maintains, the percentage of monochorionic births among the total twin-births, according to his estimate, conforms very well to the percentage of monozygotic twins among the whole twin population calculated by the differential method.

Whether any small percentage of such puzzling cases as mentioned above exists or not among twin births, accurate information on the foetal membranes is usually lacking for births outside of the hospital.

Thus, we have still to seek for the criterion for classifying twins in their physical and psychical features.

PHYSICAL FEATURES

Of all physical features, our attention is naturally directed first to physiognomy. As Dahlberg remarks (1926), we have a very sharp sense for discriminating slight details of facial appearance, so that the close resemblance of twins in physiognomy to such a degree that even near relatives can not tell them apart, must involve the identity of their various minute facial features to a very great extent. Thus physiognomy can undoubtedly serve as a good criterion for classifying twins. This method, however, has a drawback in that the judgment of the degree of resemblance depends largely on our subjective sense, and is naturally more or less arbitrary. Many workers, accordingly, seek to rely on more objective anthropological measurements and descriptions of other physical characters, such as stature, head form, hair color and form, skin color, blood group, etc.

Muller (1925), among others, has devised a scheme of calculating the a priori chance that given twins are identical on the basis of the data obtained from certain unrelated physical characters of the twins and their siblings like stature, hair form, skin color, etc. Thus, according to him,

"If there are n sibs altogether (including the twins), a of them falling into class a with respect to a given trait, b into class b, c into class c, etc., the chance that the twins should have been found in the same class is;

$$\frac{a}{n}\frac{a-1}{n-1}+\frac{b}{n}\frac{b-1}{n-1}+\frac{c}{n}\frac{c-1}{n-1}+\text{etc.}$$

If, now, the traits are inherited independently, as they usually will be to a large extent, the chance that two sibs should be in the same class in respect to all of the traits considered is the product of all these chances found in the case of each separate trait" (p. 436).

And the chance that the given twins are identical is approximately $\frac{P}{P+1}$, where $\frac{1}{P}$ stands for the chance that non-identical twins should agree in all the traits. The mathematical ground for the formula has been criticized by Miss Burks (1926) and defended by Muller (1926).

It has been remarked by certain authors that identical twins represent the right and left halves of one individual, and that there is often symmetry reversal in some feature or other. The existence of such symmetry reversal is a sign that the twins are monozygotic. Wilder (1904) and Newman (1917) have expressed their view in favor of this idea. Studies have been carried out by some workers to elucidate this interesting question of the asymmetry and symmetry reversal of twins. Handedness has been studied by Siemens (1924b), Lauterbach (1925), Dahlberg (1926) and v. Verschuer (1927), the direction of head whorl by Lauterbach (1925) and v. Verschuer (1927), the height of testes in scrotal sac by v. Verschuer (1927), besides other characters such as the mode of clasping hands and functional superiority of one leg examined by Dahlberg

(1926), asymmetry in eyes, ear-form, etc. by v. Verschuer (1927), and the occurrence of naevi by Siemens (1924b).

The result is somewhat different according to the characters considered. But symmetry reversal is rather frequent among identical twins for nearly all these characters. This is especially the case with handedness (Lauterbach, 1925; Dahlberg, 1926; v. Verschuer, 1927). But the puzzling fact is that left-handedness is decidedly more frequent among fraternal twins as well as among identical twins, than in the general population. Left-handedness ought, therefore, to be considered a phenomenon directly connected somehow with twinning in a general sense, and not necessarily with the special kind of twinning bringing about identical twins.

Siemens' diagnosis of twins (1924b, 1927), which has since been used rather extensively, is based on a good many physical features, that is

"A. Traits which agree in one-egg twins almost always and almost completely; in two-egg twins only rarely: 1. hair color and form, 2. eye color, 3. skin color, 4. downy hair of the body; B. traits which agree in one-egg twins, and which usually vary more widely among two-egg twins: 5. freckles (location of), 6. appearance of blood in the skin (teleangiectasis, cutis marmorata, acroasphyxia), 7. follicular processes (lichen pilaris, acne), 8. tongue (furrowed or not) and teeth; C. traits in which one-egg twins usually, two-egg twins only rarely show strong resemblances to each other: 9. form of face (physiognomy), 10. form of ear, 11. form of hands (and of nails), 12. body build;" besides "13. mental make-up (school standing, character, talent), 14. illness and abnormalities, 15. traits which are the bases of special methods of investigation (finger prints, microscopic comparison of the capillaries, refraction of the eyes, blood groups and so on" (Siemens, 1927, pp. 205–207).

There is no doubt that this scheme is more comprehensive and naturally safer than others hitherto proposed. It has, however, a rather limited application to twins among races in which the hair-color and form, eye color and skin color are subject to only a slight variation as, for instance, the Mongolian race.

Dahlberg (1927), lastly, puts emphasis on the usefulness of the ear form for this purpose.

FINGER, PALM AND SOLE PRINTS

Galton (1892) was the first to recognize the close similarity existing between the friction-ridge patterns of fingers of some same-sex twins. He compared the prints of fore, middle, and ring fingers of the right hand of 34 pairs of twins, and found that in some of the pairs the agreement of the patterns was so close that they should be assigned to the same class according to his classifying scheme, while in others the correspondence was only partial and in still others no correspondence was found.

Wilder (1904, 1908, 1919) worked on some 50 sets of palm and sole prints of twins, besides 16 sets of finger prints, and came to the conclusion that

"the friction-skin configuration of twins corroborates the conclusions based upon the general physical appearance, that there are two distinct types of human twins, duplicate (or identical) and fraternal." "The correspondence in the friction-skin configuration is confined to the general plan of the surface as a whole and does not extend in the least to finer details, the 'minutiae' of Galton." "In duplicate twins there is, in both hands and feet, a marked correspondence between the two sides, so that the right and left hands of each twin correspond as completely as do the right or the left hands of the two individuals. All four of the hands involved are thus duplicates of virtually the same picture, and the same phenomenon is shown in the four feet" (1919, p. 2).

Poll (1914) studied finger prints of 83 pairs of presumably identical twins besides two sets of triplets and one pair of pygopagus. In no case did he meet with a correspondence of all fingers even as regards the type of pattern. Rarely nine fingers were similar and one different.

Ganther and Rominger (1923) worked

on the finger and palm prints of five pairs of monozygotic and forty-two pairs of dizygotic twins whose placentas had been examined at birth. They found that the corresponding fingers of identical twins are usually very similar, to such an extent that at least seven, and at most nine, fingers have the same type of patterns, but at least one finger shows dissimilarity. The palm patterns of hands of identical twins show even closer resemblance; the similarity of the same side especially is very great. The palms of the dizygotic twins, on the contrary, are never so much alike. Accordingly he expressed his view that the palm prints give the most reliable criterion, next to the placenta, for identifying monozygotic twins.

Bonnevie (1923, 1924), in her studies on finger prints, examined the degree of similarity found between same-sex twins with 16 pairs of presumably fraternal and 15 pairs of presumably identical twins as material. She estimated the degree of similarity between each pair according to her own scheme, and found that the correlation of pattern-values between fraternal twins is very similar to that between ordinary brothers and sisters, whereas the correlation between the identical (?) twins is much higher, in fact so much as to "fully equal and even slightly exceed that found for the values of right and left hands of identical twins, or of single persons" (1924, p. 100).

Leven (1924) studied the finger prints of 23 pairs of same-sex twins including 15 pairs of presumably monozygotic and 8 pairs of presumably dizygotic twins. Much more difference, in the type of patterns, as well as in the number of ridges and in other details, was found among the latter than among the former kind of twins.

Lauterbach (1925), in his study on 212 pairs of twins, consisting of 149 pairs of same-sex, and 63 pairs of different-sex twins, examined the palm patterns. Special attention was given to the palm patterns of the twins showing symmetry reversal in handedness and in the whorl of the head hair. His conclusion was that "palm patterns afford no certain means of identifying monozygotic twins. Unlike-sex pairs of twins may show identity of palm patterns and reveal symmetry reversal" (p. 567).

Montgomery (1926) worked on the sole patterns of 57 pairs of same-sex, and 30 pairs of different-sex twins. He concluded that "the presence of identical patterns on the soles of a pair of twins might point to their monozygotic origin, but, as Newman states, their absence does not disprove it" (p. 299).

Kuragami (1926) examined finger-prints of 15 pairs of same-sex twins and 5 pairs of different-sex twins, and found, among other things, that in two pairs of the same-sex twins the ridgecount of the prints gave precisely the same value.

Obonai (1926) carried on a psychological and anthropological study on some 200 pairs of twins. He also examined the finger prints of these twins, and called attention to the fact that some pairs of same-sex twins which would be taken as identical judging by their resemblance in physiognomy and in physical and psychical characteristics, may have very unlike finger patterns.

Kishi (1927) collected finger prints of 60 sets of twins including 49 pairs of same-sex and 11 pairs of different-sex twins, and has found, among other things, that the finger prints of different-sex twins are more variable than those of same-sex twins.

Apart from works dealing with only a few pairs of twins, the above is, I believe, a nearly comprehensive review of the literature relating to the finger, palm, or

sole patterns of twins which has appeared to this day.

MY STUDY

The material which has formed the basis of my study consists of 9 sets of palm, sole and finger prints and 55 sets of palm and finger prints of same-sex twins, 9 sets of palm and finger prints of different-sex twins and one set of palm and finger prints of male triplets, obtained mainly from among the school children of the city of Kyoto. This material has been greatly supplemented by the collection of Mr. Obonai, who generously put them all under my examination. These include finger prints of 166 pairs of same-sex twins and 30 pairs of different-sex twins obtained from among the school children in the city and suburbs of Tokyo; and some are accompanied by palm prints.

The formulation of the patterns and ridges has been done largely after Wilder's scheme with a slight modification (Wilder, 1904, 1916; Wilder and Wentworth, 1918). Especially, it has been found advisable to take into consideration as many available characteristics of the patterns as possible. Thus, for finger patterns, besides the number of ridges, certain other characteristics, for instance, the ratio of the height and breadth and the tendency towards twisting mentioned by Bonnevie (1923, 1924), and also the length of each ridge, have been considered. For palm patterns, the number of ridges intervening between the main lines has been counted and the various shapes of the hypothenar pattern recorded. In addition to the data obtained from the examination of the above material, I have consulted, for drawing general conclusions, the data in the works by previous authors, especially by Wilder (1904, 1919), Poll (1914), Ganther and Rominger (1923), Lauterbach (1925), Montgomery (1926), Kuragami (1926) and Kishi (1927).

Fig. 1. Brothers Including a Pair of Identical Twins

The twins were born with a common chorion and placenta. Both are graduates of the Kyoto Imperial University.

Lack of space prevents me from going into the details of the study, and I can only

give very briefly a general summary of the main results.

My study has revealed that the finger, palm and sole prints of the twins whose monozygosity is evident on various grounds, such as the similarity of physiognomy, body build and school standing, resemble each

Fig. 2. Monozygotic (?) Girl-twins, from Mr. Obonai's Collection of Photographs of Twins

other closely, much more than the prints of the different-sex twins or of the same-sex twins who are identified as dizygotic. To give a rough idea of the contrast of the two kinds of twins, the finger prints of the monozygotic twins very seldom show differences in the type of pattern (whorl, twin loop, double loop, ulnar loop, etc.) in more than two pairs of corresponding fingers, whereas in dizygotic twins the difference is met with usually in more

The similarity of the pairs of monozygotic twins is especially marked between the fingers, palms or soles of the same side (right or left), so that very often the hands or feet of the same side of different individuals resemble each other more closely than the two hands or feet of the same individual. To represent in symbols, let r and l stand respectively for the right and left hand or foot of the one twin A,

Fig. 3. Boy-girl Twins very Different in Body Build; Children of a Primary School of Kyoto

and r' and l' respectively for A', the identical twin of A, then

$$r - r' \text{ (or } l - l'\text{)} < r - l \text{ (or } r' - l'\text{)}$$

Such a condition, so far as I have ascertained, is met with in no case of different-sex twins nor of same-sex twins whose dizygosity is undisputed. So that this may serve as a criterion for identifying many monozygotic twins.

To my mind, the difference in pattern of

Fig. 4a

Fig. 4b

Fig. 4. Monozygotic (?) Triplets

They are now 24 years old; enjoy good health and stood high in class; all served in the army

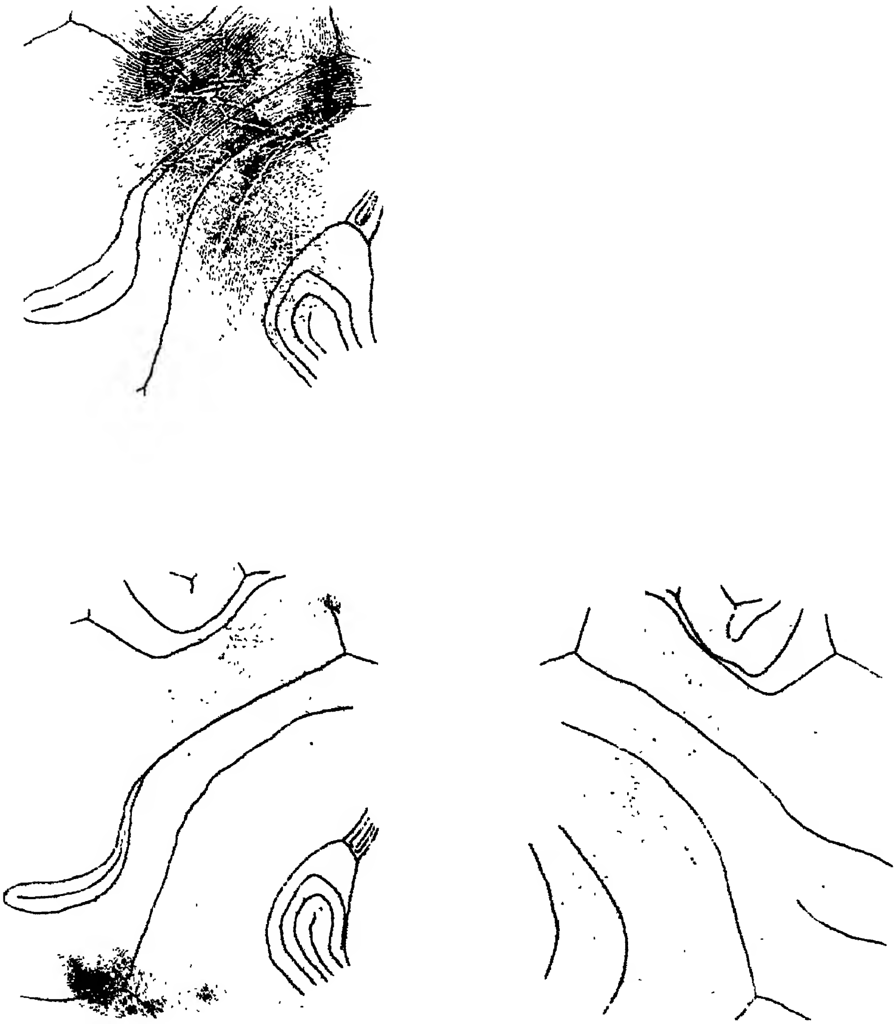


FIG. 5. PALM PRINTS OF A PAIR OF MONOZYGOTIC (?) TWINS
Note the close similarity of the patterns of hands of the same side

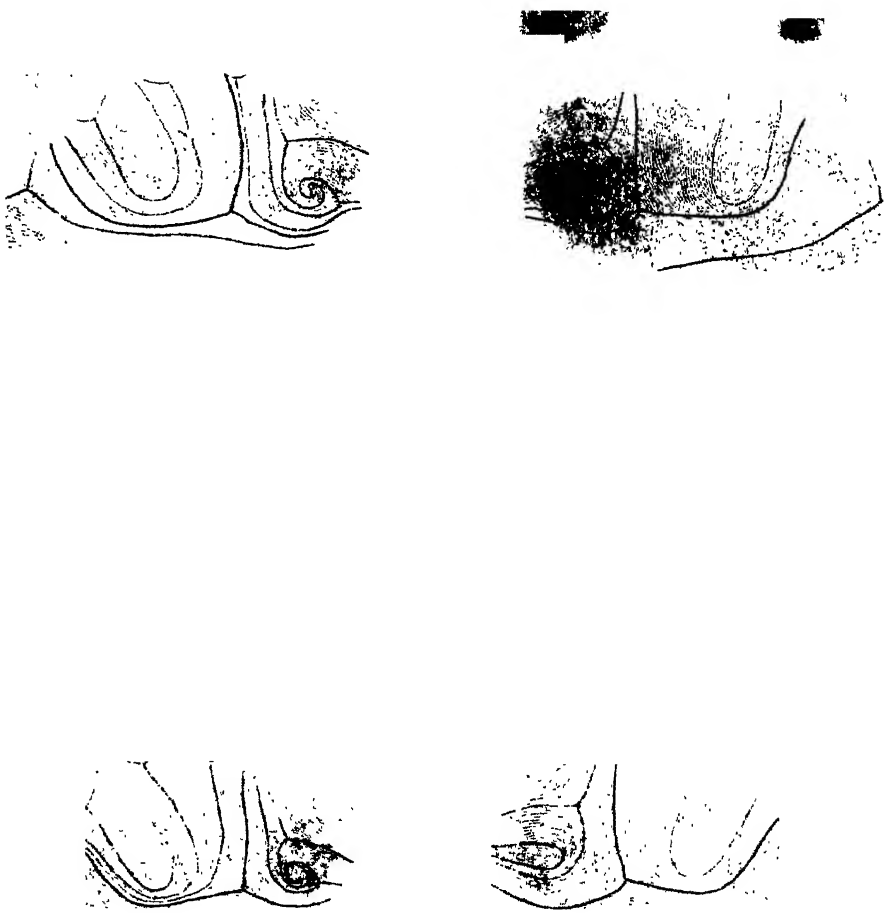


Fig. 6. Sole Prints of Another Pair of Monozygotic (?) Twins
Note the close similarity of the patterns of soles of the same side

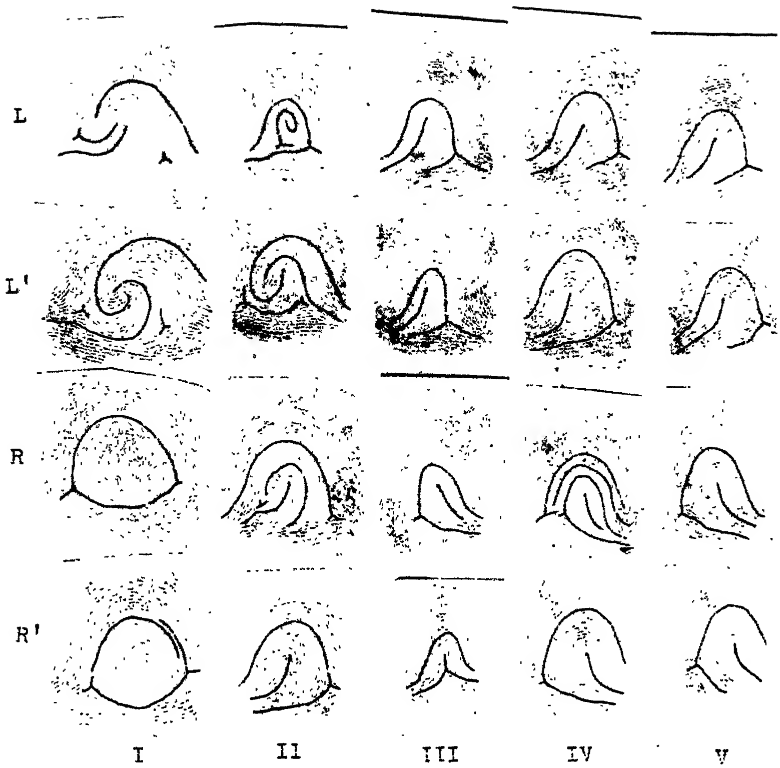


Fig. 7. Finger Prints of the Twins in Figure 1

The patterns are rather variable for monozygotic twins. Note the similarity of the patterns of thumbs of the same side.

vidual is, at least in part, due to the specialization of the right and left halves of the body, in the same sense as right or left handedness or the functional superiority of one leg, rather than to the patterns transcending the limit of control of the hereditary factor. The hands or feet of the same side of monozygotic twins, on the contrary, are virtually the duplicates of each other; and it is but natural that they resemble each other more closely than the hands or feet of one individual.

It can not be disputed, however, that certain same-sex twins who are known to have been born with a common placenta and who resemble each other very closely in physiognomy and body build, have dissimilar patterns on more than two pairs of fingers or on palms or soles. Also it is by no means rare that the general rule for patterns of monozygotic twins stated above does not hold good. The dissimilarity of the patterns or the nonconformity of them to the rule, therefore, does not necessarily disprove the monozygosity of the given twins. Thus the method of distinguishing the two kinds of twins by means of such patterns has its limitations. But, if used in collaboration with other methods, it will prove to be a very useful and reliable one for classifying twins.

LIST OF LITERATURE

(For complete bibliography see especially Wilder, 1904; Bonnevie, 1924; Siemens, 1924b; Dahlberg, 1926; and v. Verschuer, 1927).

(1) Bonnevie, K. 1923. Zur Analyse der Vererbungsfaktoren der Papillarmuster. Hereditas, 4: 211–230.
(2) ———. 1924. Studies on papillary patterns of human fingers. Jour. Genetics, 15: 1–110.
(3) Burks, Barbara S. 1926. Determining identity of twins. Jour. Heredity, 17: 193–195.
(4) Dahlberg, G. 1926. Twin births and Twins from a Hereditary Point of View. Stockholm.
(5) Galton, F. 1892. Finger Prints. London.
(6) Ganther, E., and Rominger, E. 1923. Über die Bedeutung des Handleistenbildes für die Zwillingsforschung. Zeitschr. f. Kinderheilk., 36: 212–220.
(7) Kishi, T. 1927. Sôtaizi Simon no Kenkyû (Jap.). (Studies on finger prints of twins.) Zyûzenkwai Zassi, 32, 7: 1–32.
(8) Kuragami, Y. 1926. Sôtaizi no Simon ni tuite (Jap.). (On the finger prints of twins.) Syakwai Igaku Zassi, 470: 121–130.
(9) Lauterbach, C. E. 1925. Studies in twin resemblance. Genetics, 10: 524–568.
(10) Leven, L. 1924. Über die Erbanlagen der Eineier auf Grund von Untersuchungen des Papillarliniensystems der Finger. Dermatol. Wochenschr., 78: 555–565.
(11) Montgomery, R. B. 1926. Sole patterns of twins. Biol. Bull., 50: 293–300.
(12) Muller, H. J. 1925. Mental traits and heredity. Jour. Heredity.
(14) Newman, H. H. 1917. The Biology of Twins. Chicago.
(15) Obonai, T. 1926. Sôseizi ni yoru Sinteki Iden no Kenkyû (Jap.). (Studies on Mental Inheritance of Twins.) Sinrigaku-Kenkyû, 1: 577–638.
(16) Poll, H. 1914. Über Zwillingsforschung als Hilfsmittel menschlicher Erbkunde. Zeitschr. f. Ethnol., 46: 87–105.
(17) Siemens, H. W. 1924a. Über die Eineiigkeitsdiagnose der Zwillinge aus den Eihäuten und aus dem dermatologischen Befund. Zeitschr. Induk. Abstamm. Vererb., 37: 122–124.
(18) ———. 1924b. Die Zwillingspathologie. Berlin.
(19) ———. 1925. Die Diagnose der Eineiigkeit in geburtshilflicher und in dermatologischer Betrachtung. Arch. f. Gynaekol., 126: 623–645.
(20) ———. 1927. The diagnosis of identity in twins. Jour. Heredity, 18: 201–209.
(21) v. Verschuer, O. 1927. Die vererbungsbiologische Zwillingsforschung. Ihre biologischen Grundlagen. Studien an 102 eineiigen und 45 gleichgeschlechtlichen zweieiigen Zwillings- und an 2 Drillingspaaren. Ergebnisse der Inneren Medizin u. Kinderheilk., 31: 35–120.
(22) Wilder, H. H. 1904. Duplicate twins and double monsters. Amer. Jour. Anat., 3: 387–472.
(23) ———. 1908. Zur körperlichen Identität bei Zwillingen. Anat. Anz., 32: 193–200.
(24) ———. 1916. Palm and sole studies. Biol. Bull., 30: 135–172 (I–IV), 211–252 (V–VII).
(25) ———. 1919. Physical correspondences in two sets of duplicate twins. Jour. Heredity,

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that The Quarterly Review of Biology *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* The Quarterly Review of Biology, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

MORGAN ON ENTWICKLUNGS-MECHANIK

Being a review of *Experimental Embryology* by Thomas Hunt Morgan. New York (Columbia University Press) 1927. $5\frac{7}{8} \times 9\frac{1}{8}$; xi + 766. $7.50.

By S. R. Detwiler, Columbia University, and H. B. Adelmann, Cornell University

Embryology as a scientific discipline is comparatively young. As a matter of fact, it is just a century old, since it may be said to have begun its modern epoch in 1828 with the publication of von Baer's monumental work, *Über Entwickelungsgeschichte der Thiere. Beobachtung und Reflexion.* The modern reader of this classic can only marvel at its high level of accuracy and the prophetic insight of its author.

For more than fifty years embryology remained, almost of necessity, a purely descriptive science, but with the publication of Wilhelm Roux's research concerning the time of determination of the principal axes of the frog embryo, *Ueber die Zeit der Bestimmung der Hauptrichtungen des Froschembryo,* in 1883, and his vigorous advocacy of the experimental approach to the solution of the problems of development, embryology may be said to have entered upon a new era.

This new "Zweig der Wissenschaft" was termed by Roux developmental mechanics (*Entwickelungsmechanik*). Driesch prefers to call it developmental physiology (*Entwickelungsphysiologie*), thus avoiding a mechanistic implication, but in English Experimental Embryology is the designation usually preferred. In the beginning Entwickelungsmechanik met with many obstacles, and its fond parent was frequently called upon to justify its existence and to shield it from attacks of the scornful. This he lost no opportunity to do. Numerous programs of the work were issued (1885, 1889, 1892, 1897, 1905, etc.) outlining the field. He predicted a brilliant future for the child and it is only just to say that his confidence has been abundantly justified.

As conceived by Roux, the goal of Entwickelungsmechanik is a complete causal analysis of every developmental process. While recognizing that some causal relationships might be deduced from observation, Roux laid special stress upon the value of experiments, of which he recognized four principal types: (1) the blind experiment (i.e., the I-wonder-whether-something-interesting-might-

happen-if-I-should-do-thus-and-so type of experiment); (2) the descriptive (*formal-analytische*) experiment in which no reaction is called forth in the object, (3) the indefinite causal experiment and (4) the causal-analytical experiment;—the latter being the highest type. In 1889 Roux was led to remark that "The causes of organic formations (*Gestaltungen*) are at present more unknown to us than the causes of the movements of the heavenly bodies were to mankind before Newton."

Experimental embryology is thus, as sciences go, very youthful—only forty-five years of age—a veritable youngster, and like all youngsters it is apt to be intolerant. It is prone to assume a disdainful attitude toward mere morphology, and frequently implies that its achievements are of a higher order than those of descriptive embryology. However, its more thoughtful devotees realize that, after all, there is but one science of embryology; that description must precede intelligent experiment and, furthermore, that there are many aspects of development that are not yet susceptible of experimental treatment. The importance and the need of experimental analysis must, however, be apparent to everyone.

In the forty-five years since Roux's experiment on the axes of the frog embryo, a truly enormous mass of literature dealing with experimental embryology has accumulated. Each year sees an increase in the production of literature over the preceding year, so numerous have workers in the field become. As a result, it is difficult for the beginner and even for the seasoned worker to keep fully informed of the current advances, and it becomes more and more difficult for the novice to orient himself in the subject. Summaries of research programs and reviews of the whole field from time to time are therefore exceedingly valuable.

In 1897 Professor Morgan published *The Development of the Frog's Egg. An Introduction to Experimental Embryology*. It was an admirable work, the first of its kind in the English language. At that time Roux's Archiv für Entwickelungsmechanik had been in existence only two years and but five volumes had appeared, and the Journal of Experimental Zoölogy—to mention but two sources of publication—had not yet been founded. It was then possible to give a very adequate treatment of the subject, with particular reference to the frog, in a volume of 192 pages, including a 13 page bibliography.

Since the appearance of Professor Morgan's first summary, there have, of course, been many important advances. Since 1897 more than sixty volumes of Roux's Archiv and fifty of the Journal of Experimental Zoölogy have been issued. Important research programs have been initiated and prosecuted, in many instances with gratifying success. To mention only the most fruitful, one might cite: (1) the important researches of Professor Harrison on the growth of the nerve fiber, his discovery of tissue culture and the important series of analyses of the development of the limb and other organs carried out by himself and his students, (2) the remarkable researches of Spemann and his students on the "*Organizator*" and the determination of the various organs and tissues of the Amphibian embryo, (3) the studies of artificial parthenogenesis by Loeb, Morgan, Bataillon, Brachet and others, (4) studies on cell lineage by Wilson, Conklin and others, (5) Child's development of the theory of physiological gradients, (6) the researches on cytoplasmic localizations by Conklin, Brachet and others, and (7) the development of the method of vital staining as employed by Goodale, B. G. Smith, Vogt and Goerttler in the study of the movements

of cells during gastrulation in the Amphibian, and by Detwiler and others in studying the fate of transplanted tissues. The list is not complete, nor does it necessarily cite in order of merit.

Besides several digests in foreign languages, a number of summaries in English are available. There may be mentioned Jenkinson's *Experimental Embryology* (1909), de Beer's succint and useful *Introduction to Experimental Embryology* (1926) and, particularly, the masterly chapters devoted to this subject in Professor Wilson's *The Cell in Development and Inheritance* (1925).

Since the publication of his work on the development of the frog, Professor Morgan has made a long and profitable excursion into the field of genetics and has become so intimately identified with this field that many younger investigators are apt to forget that he has been a prolific contributor to experimental embryology *sensu strictu*. In fact, he probably considers, and justly too, that he has been working in experimental embryology all the time.

And now Professor Morgan, after some years spent in pursuit of the gene, presents us with another stimulating review of experimental embryology, which has added importance in that it combines the viewpoints of the embryologist and geneticist. This time it is a volume of 766 pages containing a bibliography of 100 pages. It covers only the earlier phases of development. He promises a future volume which will consider the "more obviously physiological changes" of development, growth, reflex actions, tropisms, sex determination, embryonic grafting, influence of environment on the embryo, the source of the energy of development, etc.

As a whole, the present volume may be characterized as an eminently readable summary and analysis of the outstanding developments in the field surveyed. There are twenty-five chapters. The first is an interesting discussion of the experimental method. This is followed by seven chapters dealing with the problems connected with fertilization. There are others devoted to the physico-chemical changes in the egg after fertilization, the mechanism of cleavage, the establishment of symmetry and the origin of asymmetry, localization before cleavage and the redistribution of the visible materials of the egg by centrifuging, the development of whole or partial embryos from isolated blastomeres, the mechanics of organ formation, the fate of cells and their location, the fusion of two eggs to produce one embryo. There is a long chapter on artificial parthenogenesis and three chapters are devoted to the chromosomes of the egg and their division, the Mendelian inheritance of embryonic and larval characters and the development of species hybrids.

It is only natural that the chromosome and the gene figure prominently in the book. Professor Morgan has always realized that an adequate theory of heredity must at the same time offer a satisfactory explanation of the differentiation of the embryo. In discussing this question in *The Mechanism of Mendelian Heredity* in 1923 he stated (p. 280) that

> The cause of the differentiation of the cells of the embryo is not explained on the factorial hypothesis of heredity. On the factorial hypothesis the factors are conceived as chemical materials in the egg, which, like all chemical bodies, have definite composition. The characters of the organism are far removed, in all likelihood, from these materials. Between the two lies the whole world of embryonic development in which many and varied reactions take place before the end result, the character, emerges. Obviously, however, if every cell in the body of one individual has one complex and every cell in the body of another individual has another complex that differs from the former by one difference, we can treat the two sys-

tems as two complexes quite irrespective of what development does so long as development is orderly.

It is sometimes said that our theories of heredity must remain superficial until we know something of the reactions that transform the egg into the adult. There can be no question of the paramount importance of finding out what takes place during development. The efforts of all students of experimental embryology have been directed for several years toward this goal. It may even be true that this information, when gained, may help us to a better understanding of the factorial theory, we cannot tell; . . . . Although Mendel's law does not explain the phenomena of development, and does not pretend to explain them, it stands as a scientific explanation of heredity, because it fulfills all the requirements of any causal explanation.

He makes substantially the same statement in his *Theory of the Gene* (1926, p. 26). But in spite of the fact that he disclaims any pretension to explain differentiation on the basis of the gene theory, Professor Morgan usually gives some indication of his feelings on the subject. For instance, in 1923, he made this statement (p. 43): "Mendelian factors are not sorted out . . . . differentiation is due to the cumulative effect of regional differences in the egg and embryo, reacting with a complex factorial background that is the same in every cell."

It was with particular interest, therefore, that we examined this latest book of his to ascertain whether his ideas on this matter had been clarified and whether in this book dealing primarily with experimental embryology he would attempt to bring the theory of the gene into some closer harmony with the observed course of embryonic differentiation. It will perhaps be helpful to summarize in the briefest fashion what Professor Morgan has termed the theory of the gene, with special reference to the problem of differentiation and disregarding such aspects as linkage, etc. The theory states that the characters of the individual are represented in the chromosomes of the egg by minute entities termed the genes, which are arranged in linear order. Each gene may affect the development of many characters and the interaction of all the genes may be involved in the manifestation of any particular character. The genes are present in pairs, the members of each pair separating during maturation of the germ cell, but during the ordinary mitoses each gene is divided equally so that the daughter cells are factorially identical. It may be added that cytological evidence seems to indicate positively that the somatic mitoses are quantitative so far as the nucleus is concerned and most observers accept this as an establish fact. The problem, then, is how, with identical factorial equipment, differentiation is started, and how, when once initiated, it is brought to completion.

There would seem to be at least three factors to be considered, (1) the nucleus, (2) the cytoplasm, (3) the environment. Investigators have attempted to answer the question in different ways. The importance of the cytoplasmic localizations of the egg have been stressed, the external environment of the developing egg has been emphasized as important, and for others the nucleus is the most important element. For instance, Child has expressed himself as follows: " . . . . development of the individual represents the reaction of the factorial complex to environmental factors. This seems to be Conklin's viewpoint ('22) and it is essentially the viewpoint of the present book, according to which the physiological gradient constitutes the primary regional differential, to which the factorial complex reacts." Conklin (*In* Cowdry, *General Cytology*, '24, p. 600) emphasizes the importance of the cytoplasm as follows:

Given a definite polarity, symmetry, and pattern of the egg, all other differentiations of ontogeny could be explained as due to the interaction of non-

differentiating genes on different parts of the cytoplasm; but there is no mechanism by which embryonic differentiations could come from the action of non-differentiating genes on a homogeneous cytoplasm. The genes or Mendelian factors are undoubtedly located in the chromosomes, and they are sometimes regarded as the only differential factors of development, but if this were true these genes would of necessity have to undergo differential division and distribution to the cleavage cells, as Weismann maintained. Since this is not true it must be that some of the differential factors lie outside of the nucleus, and if they are inherited, as most of these early differentiations are, they must lie in the cytoplasm.

Rabl ('06) conceived of differentiation as brought about by a continuous interaction between nucleus and cytoplasm,—the primary germinal localizations (organ forming stuffs) of the cytoplasm furnishing the starting point. According to him both nucleus and cytoplasm are progressively changed during the process of differentiation.

Wilson, on the other hand, throws the entire responsibility upon the nucleus. "Heredity," he says, "is effected by the transmission of a nuclear preformation, which in the course of development finds expression in a process of cytoplasmic epigenesis."

Loeb ('16) viewed the cytoplasm of the egg as " 'the embryo in the rough,' carrying the genus—or even the species—heredity, while Mendelian heredity adds only the finer details to the rough block." Jenkinson ('17) adopted a similar view, holding that the larger characters are transmitted by the cytoplasm, the smaller by the nucleus. Conklin is more specific. "We are vertebrates because our mothers were vertebrates and produced eggs of the vertebrate pattern; but the color of our skin and hair and eyes, our sex, stature and mental peculiarities were determined by the sperm as well as by the egg from which we came." But as Wilson further says, "These statements are rhetorically effective, but will not stand the test of critical analysis . . . . the cytoplasmic organization of the egg *is itself the product of an antecedent process of epigenetic development* in the course of which, as we have every reason to believe, the chromosomes have played their part,—thus the chromosomes are as much concerned in the determination of the so-called 'preformed' or cytoplasmic characters as in any others."

Professor Morgan's position is very similar to that of Wilson. Starting with the assumption of a chromosomal architecture as outlined above, he brings out the following points: (1) There is no relation between the arrangement of the genes and the arrangement of the parts differentiated from the egg. (2) The genes remain intact throughout development. There is no evidence for assuming that they are altered by successive cytoplasmic differentiations. (3) There is no basis for assuming that the genes become active in a particular order nor can it be stated whether all the genes are active continually or whether some are more active than others at certain periods.

In short, about all that Professor Morgan feels sure of is that "the genes may change the cytoplasm and the cytoplasm then acts in a specific way" (p. 8).

How the chromosomes, or rather the genes that are their essential constituents alter the cytoplasm of the cells is unknown. There is at least no evidence opposed to the view that they do this by chemical processes. It is impossible to suppose that the genes themselves could be thrown off and could pass through the nuclear membrane into the cell. . . . . It is not so difficult to imagine that through their activities chemical substances are produced that find their way into the cytoplasm either at the time when the nuclear wall is dissolved and nuclear sap set free, or possibly by diffusion through the nuclear walls. (p. 198).

The genes may be influential in the formation of catalytic materials but are probably not themselves enzymes.

The evidence from matroclinous in-

heritance seems to indicate that the "genes affect the cytoplasm, not immediately in a dynamic sense, but rather by some material product that is set free from the genes into the cytoplasm" (p. 655). That there is a time element involved in the action of the genes is also indicated by other hybridization experiments, notably those of Driesch on the sea urchin.

Professor Morgan takes a decided stand against assigning organ forming properties to the various regions of the cytoplasm. While he believes that at the beginning of development the cytoplasm probably contains certain factors which initiate development, possibly determining the cleavage type, he concludes from the evidence furnished by the cleavage of egg fragments that the segmentation pattern is not foreshadowed or predelineated in the protoplasm but that the form of cleavage appears *pari passu* with the development of the mitotic spindle.

He is justly emphatic in his assertion that the visible inclusions of the cytoplasm have no organ-forming function since they may, in many types of eggs, be displaced without altering the course of development. "It does not follow, of course, that there may not be other substances that do have a determinative influence on development" (p. 493). In commenting upon the results of Conklin's experiments in which the eggs of *Styela* were placed in capillary tubes and centrifuged with the consequent formation of abnormal embryos with dislocated larval parts, he is inclined to believe that alteration of the cleavage by compression may be responsible. "Whether the yellow pigment can be separated by centrifuging from the cytoplasm in which it lies, and may then determine the local differentiation of a region, must first be demonstrated in order that crucial evidence of their differentiating function may be established" (p. 534).

In discussing spiral cleavage, a type in which the successive cleavages are more or less rigidly predetermined so that "predictable regions of the egg pass into definite cells," he states that "The alternate changes from right to left and then from left to right, etc., that are characteristic of these divisions can hardly be due to the presence of corresponding regional substances already laid down in the egg. . . . . The mosaic character of the cleavage with its accompanying localization of differentiating factors is something given, but not preformed, in the unsegmented egg" (p. 417). In other words, the various cytoplasmic regions of the egg are conceived of as predetermined in many cases, but not prelocalized.

Just what is implied by the term "differentiating factors" is not entirely clear. In certain cases, as he points out, the character of the cytoplasm seems to determine the character of the differentiation of the regions of the body as, for instance, in certain insect eggs, and as is indicated by Boveri's experiment of centrifuging the eggs of *Ascaris*, certain of Spemann's constriction experiments on *Triton*, etc.

He points out, however, that "even in such eggs where the cytoplasm plays an important rôle in determining the regional differentiation of the embryo, the character of the nuclei is also determinative for those characters that depend on their constitution" (p. 424).

It is interesting to note that symmetry and asymmetry are discussed without reference to Child's theory of physiological gradients. Professor Morgan believes that symmetry, in many cases, is impressed upon the egg by outside influences and would be loathe, we judge, to assume that it is due to an inherent property of the protoplasm in any case. We find ourselves in hearty sympathy with his statement

that while such phrases as polarity, symmetry, organ-forming germ regions, morphogenetic processes and differential cleavages may be useful when used in a descriptive sense, they become deceptive when employed as if something were explained by them. We are, after all, far from understanding the essential nature of symmetry. At present we may only describe it as it is normally manifested with its experimental alterations. Its cause we may never understand. It is, as Bateson suggested, essentially organismic pattern and may very likely have its basis in protoplasmic or molecular pattern.

For Professor Morgan, then, development would consist largely in the nuclear domination of the cytoplasm, which is responsive on the one hand to the nucleus and on the other to its external and internal environment.

One of the most interesting sections of the book is that dealing with the mutual interactions of the embryonic organs upon one another. Herbst deserves the credit for having first in 1901 clearly emphasized the importance of this field. In his *Formative Reize in der thierischen Ontogenese* he listed and discussed a number of examples of external and internal formative stimuli in ontogeny. This aspect of development was for many years more or less neglected and it is only within recent years that the work of Spemann and his students has again focused attention upon it. The fact that a neural tube or even an eye can be induced to form from belly ectoderm by an underlying implant of the roof of the archenteron or a piece of neural plate, or that a more or less perfectly organized embryo can be induced to form by implanting the dorsal lip of the blastopore, has revealed again in a most striking manner the mutual influence of embryonic parts and makes us suspect that there are undoubtedly others just as important of which we are unaware. Whether Spemann's conception of an "*Organizator*" controlling the differentiation of the embryo will stand is, perhaps, doubtful. The experiment, as Professor Morgan points out, may, at any rate, be interpreted as proving that "the formation of the neural plate depends on the presence beneath it of chorda-mesoderm and that the ectoderm of the upper hemisphere is totipotent in its responsiveness to this material."

As regards the subject of artificial parthenogenesis, a very complete summary of the work is given. The interpretation of results in this as in many other fields is still unsatisfactory. "The fact that unfertilized eggs may be induced to develop into normal embryos by artificial agents of the most diverse kind, rather than the hypotheses to account for the change, is the outstanding feature of all this work" (p. 581).

Professor Morgan is hopeful that ultimately we shall find a physical, chemical or physico-chemical explanation of all developmental phenomena. It is entirely possible that one day we shall understand fully the chemical and physical aspects of fertilization, cleavage, gastrulation and differentiation, but there would still remain to be explained the configuration of physical and chemical processes that is characteristic of the development of each organism. As Professor Kingsbury has put it

> Life in an organism today is like a tapestry in which the threads of warp and woof are woven into a pattern of exceeding intricacy and delicacy whose weaving has been going on since the beginnings of life. You may analyze the threads of process as they run in and out today in terms of chemistry and physics but the pattern stands as a history of the past and the weaving is still largely a secret of the ages.

The pattern of the genes may be cited as an example. We may describe the con-

stellation of genes peculiar to the germ-plasm of each species but it will be long before we have a causal explanation of the gene pattern of each particular germ-plasm.

In surveying the status of experimental embryology today one cannot fail to be impressed with the fact that as yet but few causal explanations of developmental processes have been established. Only a small percentage of the experiments described are really causal-analytical in Roux's sense; the bulk of them would have to be described as descriptive experiments and not a few would fall into his category of blind experiment. However, the main service of many experiments, as Professor Morgan has pointed out, has been to reveal new possibilities and the outlook for further advance has never been brighter then at present. One of the great services which Professor Morgan has rendered us in writing his book has been to point out clearly the limitations of many experimental procedures and to suggest other attacks and new problems for solution. The book will prove therefore, a stimulus to many future types of work. We look forward eagerly to the second volume.

Fortunately, perhaps, von Baer's statement is as applicable today as it was in 1828:

> Noch manchem wird ein Preis zu Theil werden. Die Palme aber wird der Glückliche erringen, dem es vorbehalten ist, die bildenden Kräfte des thierischen Körpers auf die allgemeine Kräfte oder Lebensrichtungen des Weltganzen zurückzuführen. Der Baum aus welchem seine Wiege gezimmert werden soll, hat noch nicht gekeimt.

BRIEF NOTICES

EVOLUTION

THE EVOLUTION OF MAN SCIENTIFICALLY DISPROVED. *In 50 Arguments.*
By William A. Williams.
Rev. William A. Williams
1202 Atlantic Ave., Camden, N. J.
$1.00 5 x $7\frac{1}{2}$; 127

The Reverend Dr. Williams has written such a book as to justify his inclusion in our Fundamentalist Portrait Gallery. We take great pleasure in presenting him to the readers of THE QUARTERLY REVIEW OF BIOLOGY. He is an Ex-president of Franklin College, Ohio, author of "Early American Families," "Silver Tones," "Song Jewels," etc.

The Evolution of Man Scientifically Disproved was first published in 1925, and republished, in a revised and "corrected"

edition of 20,000 copies, in 1928. So it can be seen that the book has had at least a moderate success. And this success seems to us warranted. For the book is by a long way the most amusing Fundamentalist tract that has come our way. What makes it amusing is that its technique is so pesky mean. The strategy is to discuss the numerical consequences of various general statements which have been made by scientific men regarding some of the variables involved in the arguments in favor of evolution. In all controversial technique one of the most devilish, and often devastating, tricks is to set forth solemnly the simple numerical results which necessarily (or supposedly necessarily) follow upon general statements. When someone engrossed in a particular line of evidence which he has been studying says casually that man has been upon the earth one million years, or one hundred thousand years, or some other long time, he usually overlooks the fact that a zealous and ingenious person can figure with pencil and paper about this statement in a whole lot of ways that its originator never thought about at all. Sometimes the consequences of such purposeful arithmetic may be embarrassing in high degree. It was by this technique that the good Bishop Colenso opened the flood gates of Modernism and the Higher Criticism when he turned his diabolical arithmetic loose upon the Pentateuch.

It is again precisely this sort of thing that the Rev. Dr. Williams has done to the evolutionists. His book is divided into three parts. The first part has for its general title "The Evolution of the Human Body Mathematically Disproved;" the second part, which, along with the third, appears to have been written at some later date than the first, has for its title "Evidence Answered;" finally, the third part has to do with "The Soul."

The initial calculation runs this way:

> The population of the world, based upon the Berlin census reports of 1922, was found to be 1,804,187,000. The human race must double itself 30.75 times to make this number. This result may be approximately ascertained by the following computation:
>
> At the beginning of the first period of doubling there would just be two human beings; the second, 4; the third, 8; the fourth, 16; the tenth, 1024; the twentieth, 1,048,576; the thirtieth, 1,073,741,824; and the thirty-first, 2,147,483,648. In other words, if we raise two to the thirtieth power, we have 1,073,741,824; or to the thirty-first power, 2,147,483,648. Therefore, it is evident even to the school boy, that, to have the present population of the globe, the net population must be doubled more than thirty times and less than thirty-one times. By logarithms, we find it to be 30.75 times. After all allowances are made for natural deaths, wars, catastrophes, and losses of all kinds, if the human race would double its numbers 30.75 times, we would have the present population of the globe.
>
> Now, according to the chronology of Hales, based on the Septuagint text, 5077 years have elapsed since the flood, and 5177 years since the ancestors of mankind numbered only two, Noah and his wife. By dividing 5177 by 30.75, we find it requires an average of 168.3 years for the human race to double its numbers, in order to make the present population. This is a reasonable average length of time.
>
> Moreover, it is singularly confirmed by the number of Jews, or descendants of Jacob. According to Hales, 3850 years have passed since the marriage of Jacob. By the same method of calculation as above, the Jews, who, according to the Jewish yearbook for 1922, number 15,393,815, must have doubled their numbers 23.8758 times, or once every 161.251 years. The whole human race, therefore, on an average has doubled its numbers every 168.3 years; and the Jews, every 161.251 years. What a marvelous agreement!

So far so good. Leaving Dr. Williams' calculations to one side for a moment and making some of our own, it is a fact that between 1650 and 1920 (= 270 years) the population of the world increased about 3.7 times. In other words, during this period of reasonably reliable estimates of world population it has doubled at the rate of once in approximately 146 years. This is a figure of at least roughly the same

order of magnitude as Dr. Williams' more pious ones. A calculating astronomer practicing his own trade would regard it, all things considered, as about equivalent to close agreement.

Let us now return to the reverend gentleman's arithmetic, which we personally believe to have been inspired by the Prince of Darkness and not by God, as Dr. Williams thinks:

> Now the evolutionists claim that the human race is 2,000,000 years old. There is no good reason for believing that, during all these years the developing dominant species would not increase as rapidly as the Jews, or the human race in historic times, especially since the restraints of civilization and marriage did not exist. But let us generously suppose that these remote ancestors, beginning with one pair, doubled their numbers in 1612.51 years, one-tenth as rapidly as the Jews, or 1240 times in 2,000,000 years. If we raise 2 to the 1240th power, the result is 18,932,139,737,991 with 360 figures following. The population of the world therefore, would have been 18,932,139,737,991 decillion, decillion, decillion, decillion, decillion, decillion, decillion, decillion, decillion, decillion; or 18,932,139,737,991 vigintillion, vigintillion, vigintillion, vigintillion, vigintillion, vigintillion.
>
> Or, let us suppose that man, the dominant species, originated from a single pair, only 100,000 years ago, the shortest period suggested by any evolutionist (and much too short for evolution) and that the population doubled in 1612.51 years, one-tenth the Jewish rate of net increase, a most generous estimate. The present population of the globe should be 4,660,210,253,138,204,300 or 2,527,570,733 for every man, woman and child!

This is intended by Dr. Williams to make the evolutionist stop and think. But he has still more heavy artillery. What of this:

> Now, if there had been no flood to destroy the human race, then the descendants of Adam, in the 7333 years, would have been 16,384 times the 1,804,187,000, or 29,559,799,808,000; or computed at the Jewish rate of net increase for 7333 years since Adam, the population would have been still greater, or 35,184,372,088,832. These calculations are in perfect accord with the Scripture story of the special creation of man, and the destruction of the race by a flood. Had it not been for the flood, the earth could not have sustained the descendants of Adam. Is not this a demonstration, decisive and final?

Here we stop. There is a great deal more that might be said about this book, but all that we care to do in this review is to expose the Reverend Doctor's technique in the hope that it will whet the reader's appetite. He has corresponded with a good many of the doughtiest Anti-fundamentalist warriors and the quotations he prints from their letters make highly amusing reading. Why *do* people write silly answers to idiotic letters?

We want to close this review with a serious word. The numerical consequences of any theory of organic evolution, in respect of practically any particular whatever, have never been seriously or exhaustively studied by a competent mathematician. Such exceptions to this statement as are furnished by the work of Karl Pearson and J. B. S. Haldane, and a few others, fine as they are within their limitations, are trivial in comparison with the vastness of the problem really involved. Until adequate research along these lines has proceeded much farther than it has now, and until many more biologists are able than now are to comprehend what the problem really means, and to read intelligently contributions towards its solution, it is to be expected that we shall be confronted from time to time with theological arithmetic of the sort assembled in this book. *But*, in our humble opinion, it will be poor tactics on the part of scientific men to attempt to meet such cases by calling the authors names, or by brushing the matter lightly aside as misguided nonsense. For the truth is that any theory of evolution *does have* necessary numerical consequences, and until we know better than we now do just what these are for any particular

theory of evolution we happen at the time to be enamored of, it would seem the part of wisdom to be cautious in our handling of the other fellow's computations.

EMERGENT EVOLUTION AND THE SOCIAL.
By William Morton Wheeler.
Kegan Paul, Trench, Trubner and Co., Ltd.
2s. 6d. $3\frac{3}{4}$ x 6; 57 *London*
EMERGENT EVOLUTION AND THE DEVELOPMENT OF SOCIETIES.
By William Morton Wheeler.
W. W. Morton and Co., Inc.
\$1.00 $4\frac{1}{4}$ x $6\frac{1}{2}$; 80 *New York*

These are the English and American editions respectively of a notable little book, which begins with Professor Wheeler's address given before the International Congress of Philosophy. The main idea is that when previously separate, distinct, and self-contained things combine together, the "whole" which emerges is usually something quite different from the mere sum of the things which combine to make it. For example, a person with the most extensive knowledge conceivable about hydrogen and oxygen alone could not possibly have predicted in advance of the trial that the result of combining two parts of the former gas with one of the latter would be that remarkable and useful substance, water, which is not a gas at all but a liquid—an obviously different kind of thing. Water, in short, is an emergent, something new and different. So also is a colony of ants, or bees, or the Republican National Committee. What such groups do, as wholes, is often or always quite different from what could be predicted by mere summation of the separate behaviors of their individual members.

The most important emergent levels in the course of evolution are usually listed in ascending order as space-time, matter, life, mind, and deity. Professor Wheeler thinks, in view of the "profuse and unabated emergence of idiots, morons, lunatics, criminals, and parasites in our midst," the prospect of the emergence of deity is "about as imminent as the Greek Kalends." He elaborates with great plausibility the idea that an important emergent level next in ascending order above mind is the social. Societies he regards as super-organisms. They behave in purposeful ways as wholes.

Not only is this brilliant little book valuable on account of its contribution to the theory of society, but it also gives a clearer picture to the general reader of the content and significance of the whole doctrine of emergent evolution than any other book of anything like the same brevity that has yet appeared.

THE SPECIES PROBLEM. *An Introduction to the Study of Evolutionary Divergence in Natural Populations.*
By G. C. Robson. *Oliver and Boyd*
15 shillings net *Edinburgh*
$5\frac{1}{2}$ x $8\frac{3}{4}$; vii + 283

An extremely interesting and valuable discussion of evolution written by a systematist and field naturalist. Of late years it has been chiefly the laboratory geneticist and the paleontologist who have discussed the subject, and it is therefore refreshing to hear talk about the origin of species by one whose professional business it is to deal with them at first hand on a large scale. The first chapter is devoted to a discussion of the various criteria which have been used to distinguish species. It is shown that none of these is completely satisfactory, and that the different ones fail to coincide completely in the results to which they lead.

The following topics are then taken up: The constitution of species and natural populations; physiological differentiation; the distribution of allied species; isolation as a factor in the divergence of species; the origin and spread of variant characters; correlation and the origin of groups. There is a bibliography covering 19 pages.

This book is a contribution of first-rate significance to the literature of evolution.

PALAEOBIOLOGICA.
Edited by Othenio Abel (with collaboration of Fritz Drevermann, Otto Jaekel, Franz Baron Nopcsa, and Jan Versluys.)
Emil Haim and Co.
50 marks (paper) *Wien*
53 marks (cloth)
$6\frac{3}{4}$ x $9\frac{1}{2}$; iv + 376

A *Festschrift* in honor of Louis Dollo, on the completion of his seventieth year of life. It contains 28 papers on a wide variety of subjects in the general fields of palaeontology, comparative anatomy, and evolution, by distinguished workers on these subjects in various parts of the world. The volume is beautifully printed and illustrated, and does great credit to the publisher as well as to the editor. This *Festschrift* constitutes the first four parts of the first volume of a new journal to be devoted to palaeontology.

GENETICS

DIE ERGEBNISSE DER GENETISCHEN WEIZENFORSCHUNG.
By Birger Kajanus. *Martinus Nijhoff*
5 guilders *The Hague*
$6\frac{1}{4}$ x $9\frac{5}{8}$; 104 (paper)

This monograph, published in *Bibliographica Genetica* (III, 1927), reviews the literature on the genetics of wheat up to, and including, the year 1924. There is a bibliography of 214 titles.

HANDBUCH DER VERERBUNGSWISSENSCHAFT. *Lieferung 1. Band III.* Containing following articles: *Entwicklungsmechanik und Vererbung bei Tieren*, by *W. Schleip*, and *Partielle Keimesschädigungen durch Radium und Röntgenstrahlen*, by *P. Hertwig.*
Gebrüder Borntraeger
9.60 marks 7 x $10\frac{1}{2}$; 129 (paper) *Berlin*

Since the beginning of this century genetics has reached one of the first places among the branches of biological science. The tremendous growth of genetic literature published in all parts of the world, not only in special journals but in general biological and scientific periodicals, will soon make it really impossible for the average biologist to keep in touch with the progress in the different special lines of this subject. Textbooks on heredity have not the proper dimensions to fulfill this requirement.

The purpose of the *Handbuch* planned by Professors Baur and Hartmann is to review the whole field of modern genetics. Up to the present time no such work has been attempted. The material will be divided according to special problems and not according to groups of animals and plants, as was done by Lang (*Die experimentelle Vererbungslehre in der Zoölogie seit 1900*), and by several authors in the well-known *Bibliographia Genetica.*

The three volumes of the *Handbuch* will be made up of thirty-three sections, by twenty-nine collaborators, most of whom are well known German biologists, although the names of H. J. Muller (U. S. A.), J. Nilsson-Ehle (Sweden), and H. Federley (Finland) are included in the list.

The content of the *Handbuch* is broader than the title implies. The last volume will contain sections on evolution, the phylogeny of animals and plants, and the origin of domesticated animals and plants. A number of sections will be devoted to the applications of genetics: eugenics, and plant and animal breeding. When finished the *Handbuch* will be an indispensable reference book in the libraries of university biological laboratories, experiment stations, and individual workers in the fields of human, animal, and plant heredity.

The first section, now published, presents an attempt to connect the modern science of heredity with *Entwicklungsmechanik*—the physiology of development. It must be admitted that there is an obvious difficulty in correlating the two lines of investigation: the highly developed genetic theory, which permits us to predict with a very great degree of accuracy the characteristics of progeny in our hybridization experiments, on the one hand, and, on the other, an understanding of the mechanism by which the genes control the development of a growing organism.

The second part, written by Dr. Paula Hertwig, discusses one of the most interesting problems of present day genetics. It deals not only with the influence of radium and Röntgen rays, as may be learned from the title, upon the germ cells, but includes also a short review of experiments with other agencies. It should be noted that the discussion of the latter is far from complete. For instance, the well-known, although not entirely conclusive, temperature experiments of Standfuss, Fischer, etc., are not even mentioned. We should also prefer not to use the term "*Keimesschädigungen*" in describing the experiments on the influence of external agencies upon the germ cells, because it implies a certain amount of subjective judgment of the harmfulness of the effect. A neutral term *Keimesbeeinflussungen*, would be preferable.

ENTSTEHUNG DER HAUSTIERE. *Handbuch der Vererbungswissenschaft. Lieferung 2 (III, K)*
By B. Klatt. *Gebrüder Borntraeger*
15 marks 7 x $10\frac{1}{2}$; 107 (paper) *Berlin*

This number of the Baur-Hartmann *Handbuch* is devoted to a thorough discussion, well illustrated, of the origin of the common domesticated animals, and of the modifying effects of domestication upon their structures and functions. There is a bibliography of eight pages.

THE PROSPECTIVE DEVELOPMENT OF PERU AS A SHEEP-BREEDING AND WOOL-GROWING COUNTRY.
By Aldred F. Barker. *Granja Modelo Puno Chuquibambilla, Peru*
$7\frac{1}{8}$ x $9\frac{3}{4}$; xii + 174 (paper)

A report to the Peruvian government, by the Professor of textile industries at Leeds, which is of considerable interest and value to students of the genetics of sheep and wool.

GENERAL BIOLOGY

LA CONQUÊTE DE LA VIE.
By Serge Voronoff. *Eugène Fasquelle*
12 francs $4\frac{3}{4}$ x $7\frac{1}{2}$; 228 (paper) *Paris*

In his latest volume Dr. Voronoff says about the same thing over again about his rejuvenation technique. We like the author's ideal, even if we are sceptical about its realization through testicular transplantation: "L'idéal vers lequel tendent nos efforts, c'est de conserver la vie

dans la plénitude de ses manifestations physiques et intellectuelles, d'abréger le temps de la vieillesse, et de reculer la mort à ses dernières limites. VIVRE JEUNE!"

In connection with Dr. Voronoff's work the readers of The Quarterly Review of Biology will be interested in the report of an official investigation, recently issued by the Board of Agriculture for Scotland, on his animal experiments. A commission consisting of Dr. F. H. A. Marshall and Dr. A. Walton of Cambridge, and Dr. F. A. E. Crew and Mr. W. C. Miller of Edinburgh, went to the experimental farm in Algeria and studied the material in the experiments there under way. The commission was not satisfied that Dr. Voronoff had proved his thesis, either in the case of the rejuvenated bull or the grafted rams.

L'ORIGINE DE LA VIE. *La radiation et les êtres vivants.*
By Georges Lakhovsky.
Gauthier-Villars et Cie
20 francs $5\frac{1}{4} \times 7\frac{5}{8}$; 175 (paper) *Paris*
CONTRIBUTION À L'ÉTIOLOGIE DU CANCER.
By G. Lakhovsky. *Gauthier-Villars et Cie*
20 francs *Paris*
$9\frac{1}{2} \times 12\frac{5}{8}$; 12 + 4 plates (paper)

Dr. Lakhovsky's general idea is that the living cell is an elemental electric oscillator, which absorbs and emits electromagnetic radiations. Life is nothing other than the manifestation of this oscillatory state of the cell. In a state of health there is equilibrium between the waves absorbed and the waves emitted. Disease is electromagnetic disequilibration.

This will sound pretty dubious to the biologist generally speaking. But this is to be said; Dr. Lakhovsky is not one of those who speculates and lets it go at that, endeavoring merely to fortify the weakness of his case by the luxuriance of his verbosity. He researches, both by the experimental and the statistical route, and has brought to light in this way some curious things about cancer death rates, and plant cancers, in relation to cosmic rays, as he supposes. We direct particular attention to his most recent paper (at least to come to our attention) in the *Comptes Rendus*, 11 April, 1928. No experimentalist will be in the least convinced by the results there recounted, but perhaps the paper will stir some one up to repeat the experiments with some methodological precision. Also the curious correlations between cancer death rates and the character of the soil discussed in the second of the books here noted is interesting, but, alas, probably not significant.

A SHORTER PHYSICAL GEOGRAPHY.
By Emmanuel de Martonne. Translated from the French by E. D. Laborde.
Alfred A. Knopf, Inc.
\$4.00 $5\frac{1}{2} \times 8\frac{3}{4}$; xvi + 338 *New York*

This book is primarily intended for teachers of physical geography, but the ecologists will find it useful in their work as a reference work, and for assigned collateral reading. Throughout the book the author, who is regarded as the leading exponent of physical geography in France, never loses sight of the fact that his subject is physical geography, and each phase is dealt with strictly from that point of view. He has judged to a nicety the amount of geology and physics necessary to build up geographical principles. Likewise, when he comes to the treatment of that part of the book dealing with plant and animal life his point of view is strictly geographical. At the end of each

general division of the book there is an appendix giving suggestions for further reading and for practical work demonstrating the important features under consideration. An excellent index adds to the usefulness of the book.

BIOLOGY OF THE VERTEBRATES. *A Comparative Study of Man and His Animal Allies.*
By Herbert E. Walter. *The Macmillan Co.*
$5.00 $5\frac{1}{2} \times 8\frac{1}{2}$; xxv + 788 *New York*

This excellent textbook is the outgrowth and embodiment of a course in vertebrate comparative anatomy which Professor Walter has taught for many years. It develops the subject along novel lines, and really justifies its main title. It is just as sound as the old Wiedershein text on which we were all nurtured a quarter of a century ago, and a great deal more interesting. Tastes will differ about the advisability of the occasionally journalistic diction and headlining in which the author has chosen to write. But after all this is only a matter of taste. The book is, regardless of its stylistic peculiarities, a valuable and original contribution to the elementary teaching literature of biology. There is only a short derivative bibliography, but the book is well indexed.

THE RATE OF LIVING. *Being an Account of some Experimental Studies on the Biology of Life Duration.*
By Raymond Pearl. *Alfred A. Knopf, Inc.*
$3.50 $5\frac{1}{2} \times 8$; v + 185 *New York*

This book, which embodies a series of lectures delivered at University College, London, summarizes and puts together in orderly fashion the results of the author's experimental studies on duration of life, carried out since 1920, with *Drosophila* and seedlings of *Cucumis melo* as the material chiefly used. Following introductory discussions of the history of the subject and the technique used in the experimental work, successive chapters deal with life tables for *Drosophila;* the effect of density of population on duration of life; the inheritance of longevity; inherent vitality; and the relation of total duration of life to the rate of vital activities. The general conclusion reached is that duration of life varies inversely as the rate of energy expenditure during its continuance. There is a bibliography of 141 titles.

DIE ÄTIOLOGIE DER BÖSARTIGEN GESCHWÜLSTE. *Nach dem gegenwärtigen Stande der klinischen Erfahrung und der experimentellen Forschung.*
By Carl Lewin. *Julius Springer*
18 marks *Berlin*
$6\frac{3}{4} \times 10\frac{1}{4}$; viii + 231 (paper)

A thorough, critical review of the work which has been done in the search for the cause of cancer. The author finds that the present status of investigation in this field does not warrant any final conclusion. There is a bibliography covering 24 pages. The general biologist will find this volume useful in orienting himself in regard to this vast experimental and clinical literature. Unfortunately there is no index.

ANIMAL BIOLOGY.
By J. B. S. Haldane and Julian Huxley.
Oxford University Press
$2.50 $4\frac{7}{8} \times 7\frac{3}{8}$; xvi + 344 *New York*

An elementary textbook of general biology which departs widely from the conventional, both in respect of emphasis and mode of treatment of the different subjects. As would be expected from the

senior author's predilections greater space and much more adequate treatment than is usual in textbooks fall to the functional as contrasted with the morphological aspects of general biology. It is a brilliantly written volume, which will find perhaps even greater usefulness as an introduction to the subject for the adult layman, than as a school textbook, though in the latter rôle its position is outstanding.

THE EFFECT OF AQUEOUS EXTRACTS OF TAR ON DEVELOPING TROUT OVA AND ON ALEVINS. *Fishery Investigations. Series I. Vol. III. No. 2.*
By A. C. Gardiner. *H. M. Stationery Office*
1s. 3d. $7\frac{1}{4} \times 10\frac{3}{4}$; 14 (paper) *London*

One volume of Road Board Tar was agitated for 18 hours with 3 volumes of water to form a stock solution. One part of stock solution to 10 volumes and to 50 volumes of water formed strong and dilute test solutions. The results showed that such tar extracts were wholly without effect upon ova and very young fry, but with advancing age the susceptibility to poisoning increases, so that fry 110–115 days old could not stand more than 15 minutes immersion in a solution of 40/100,000 phenol. Even so they had greater resistance than yearling trout.

DIE GEWEBEZÜCHTUNG IN VITRO.
By V. Bisceglie and A. Juhász-Schäffer.
Julius Springer
24 marks (paper) *Berlin*
25.40 marks (bound)
$5\frac{3}{4} \times 8\frac{5}{8}$; viii + 355

This useful treatise constitutes Volume 14 of the series of *Monographien aus dem Gesamtgebiet der Physiologie der Pflanzen und der Tiere.* It reviews the now extensive literature which exists on the technique and results of tissue culture *in vitro.* There are 71 illustrations, and an extensive bibliography, covering some 42 closely printed pages.

ÜBER DEN TOD.
By Georg Perthes. *Ferdinand Enke*
2.80 marks *Stuttgart*
$6\frac{1}{2} \times 9\frac{5}{8}$; 73 (paper)

The second edition of a pamphlet which contains two essays on the general subject of senescence and death. The first is a discussion of the manner of death. The second, which is a posthumous publication, deals with the general biology of death.

INDEX BIOLOGORUM. *Investigatores. Laboratoria. Periodica.*
Edited by G. Chr. Hirsch. *Julius Springer*
27 marks $5\frac{3}{8} \times 8\frac{1}{8}$; vi + 545 *Berlin*

This is an extraordinarily useful and well-edited international Who's Who of workers in the biological sciences. It seems rather expensive, considering its size and the considerable sale which it is sure to have, but it is well worth the money as a clerical assistant in any laboratory or library. The sub-title indicates its scope.

DE LAMAR LECTURES 1926–1927. *The Johns Hopkins University, School of Hygiene and Public Health.*
The Williams & Wilkins Co.
\$5.00 6 x 9; 223 *Baltimore*

These lectures are chiefly of interest to the public health worker and the medical man. But one will be welcomed by the general biologist. Dr. G. H. F. Nuttall, Quick professor of biology in the University of Cambridge, discourses in a most

entertaining manner about "Some pioneers in parasitology."

HUMAN BIOLOGY

THE AMERICAN NEGRO. *A Study in Racial Crossing.*
By Melville J. Herskovits.
Alfred A. Knopf, Inc.
$1.75 5 x 7½; xiv + 92 *New York*

This little book furnishes an excellent summary, in readable form comprehensible to the lay reader, of the results of the important studies that Dr. Herskovits has been making during the past four or five years on the anthropology of the American negro. The work has been carefully and thoroughly done, and therefore the conclusions reached are worthy of serious consideration. They run counter to a whole flock of preconceptions of geneticists and eugenists. Let it first be noted that Dr. Herskovits has worked with "run-of-mine" negroes, chiefly in Washington, D. C., in respect of whom it is idle to talk about "pure" negroes, or "first crosses" between white and negro. "The population we have considered is not the first nor even the second filial generation, in the main, but is farther removed from the original crossing."

Now for the results.

> What we see is that in trait after trait the average is about half-way between the averages for the White population and the African, so that what we have represented here is a blend, if the gross statistical analysis is correct. In the second place there would have to be an increase in variability if the Mendelian hypothesis were operative in this case. But I need not repeat the fact that the American Negro is homogeneous, and that the index of this homogeneity is the low variability of trait after trait when this variability is compared with that of the so-called "pure" populations. Results such as these must give us pause. It may be that Mendelian heredity is operating in a way so complex that it cannot be discerned by the use of statistical analysis of adult groups, although this type of material constitutes by far the greatest portion of that available. When the actual heredity from parents to children is investigated, a new light may be thrown on the situation. But the data which have gone into this study of the American Negro thus far do not seem, when analyzed, to show any tendency to act according to the requirements of the Mendelian hypothesis.

We heartily commend this entertaining and significant little volume to our readers.

A STUDY OF RACES IN THE ANCIENT NEAR EAST.
By William H. Worrell.
D. Appleton and Co.
$3.00 5½ x 8½; xiv + 139 *New York*

In brief space the author of this interesting volume, who is Associate Professor of Semitics in the University of Michigan, brings to bear geographic, ethnologic, and linguistic evidence upon the problem of the disentanglement of the knotty skein of race in the Near East. At the start he states that the book is the outcome of a

> life-long romantic interest in race, which has been fed and deepened by long contact with the Jewish people of many lands. They are The Race. As I stand before these faces, representing many types, I fancy I see in real presence Hittite and Babylonian, Canaanite and Aramaean; now all "Jews," many American citizens, some eminent in modern life, speaking the Germanic-Romance language of the British Isles, or the medieval German of the Rhineland, or the Spagnoli and Arabic of Moorish Spain. Once, I know, their forebears wrote works in Arabic, and before that in Hellenistic Greek and Aramaic, and before that in Hebrew. They came out of Arabia, the fountain-head of Semitic speech. Behind the intricacies and mysteries of Arabic lie the revelations of ancient Akkadian and Ethiopic. But this is only the beginning: The pictured monuments of Egypt tell us that the most archaic Semitic speech is no more than an early offshoot of a trunk whose branches even now flourish all over Africa. With this type of speech there went a race which by degrees we trace back to the Atlas highlands. We

fancy we can almost follow them across into Europe, and imagine them the builders of Stonehenge and the dolmens of Brittany. Perhaps they were the people of Druidism. It may be that Caesar's soldiers heard in Aquitania the last echoes of European Hamitic speech; and that Goidels and Brythons learned from Pictish mothers the idioms of this pre-Aryan British tongue. And may not this have been indeed, the language of the whole Mediterranean race?

The book includes a number of excellently chosen photographs of racial types. Altogether it is a valuable addition to the literature on a particularly puzzling problem in the biology of human races.

HEREDITY AND HUMAN AFFAIRS.
By Edward M. East. Charles Scribner's Sons
$3.50 6 x 8¾; vii + 325 *New York*

This book is, without doubt, the best presentation of the eugenic position that has yet been prepared for the general reader. Professor East has all the requisites for producing such a book; a commanding position among scientific students of genetics; a wide knowledge of human biology; and the ability to write with clarity and vigor.

The wide scope of the book is indicated by the chapter headings: Science and the new era of humanism; heredity—late master riddle of science; the machinery of heredity; the grammar of heredity; heredity and sex; the inheritance of human types; the two collaborators—heredity and environment; marriage between near kin; racial traits; some specific race problems; genius, mediocrity, and education; the lower levels of humanity; the survival of the underman; immigration; the problems of every-day life.

There is thorough documentation throughout. The writer of this notice does not agree with Professor East's position on a number of eugenic matters, and probably there are other biologists who do not. But this is a point of no particular consequence. The important thing is that in this book we have a competent, authoritative, well written exposition of the present status of eugenic science, which will not only inform the public but also be of great help to every worker in this field as a reference source.

ACCRESCIMENTO CORPOREO E COSTITUZIONI DELL'UOMO.
By Luigi Castaldi. *Luigi Niccolai*
50 lire *Florence*
6⅞ x 9¾; viii + 350 (paper)

This is a contribution to human biology in general, and to constitutional morphology in particular, of real interest and importance. In several respects it must be regarded as a model for scientific investigation in the field of constitutional morphology, however much any particular reader may be inclined to disagree with particular details. The literature is extensively and intelligently reviewed as a background to the author's own researches on human growth. The scope of the book is indicated by the following list of the main divisions of the treatment: Definition of body growth; methods for the biometrical study of growth; prenatal growth of the body as a whole and of the principal viscera; postnatal growth of the body as a whole; postnatal growth of the principal viscera; the results of growth as expressed in ideal types, and in constitutional morphological types; the growth of cells and tissues; causal factors in the corporeal growth of man (endocrines, etc.); anomalies and disharmonies of growth; some eugenic considerations.

The book is very well indexed and abundantly illustrated. We heartily commend it to our readers as a stimulating and interesting contribution.

FOOTPRINTS OF EARLY MAN.
By Donald A. Mackenzie.
Blackie and Son, Ltd.
5 shillings *Glasgow*
$5\frac{1}{4} \times 7\frac{5}{8}$; xviii + 190

In this readable, if not very deep, book the author has brought together brief descriptions of all of the more important records that have been left by ancient man. Sand and gravel pits, asphalt beds and caves have furnished contributions to our knowledge of prehistory. Based upon these discoveries the author reconstructs what he conceives to be the customs, modes of living and wanderings of primitive man. The narrative is brought down to the dawn of what we still oddly call the "historical" period. Summaries are given of the archeological finds made by recent expeditions to China and the Gobi Desert, as well as descriptions of the recent discoveries of the Galilee, Rhodesian and "Lady of Lloyds" skulls.

This book, being in no way technical, will be of interest to the general reader. The volume is illustrated by 16 plates, and a brief bibliography of one page is given, containing a list of the chief works of reference consulted by the writer.

THE RACIAL ELEMENTS OF EUROPEAN HISTORY.
By Hans F. K. Günther (Translated from the second German edition by G. C. Wheeler).
E. P. Dutton and Co.
\$4.60 $5\frac{1}{2} \times 8\frac{5}{8}$; vi + 279 *New York*

The early chapters of this book deal with an analysis of the population of Europe into five distinct types or races. The analysis is made chiefly by means of anthropometric measurements, but mental traits are likewise considered. Much stress is put upon the importance of the correlation of certain characteristics in obtaining a true picture of the several races making up a population. Considerable space is devoted to the European races (particularly the Nordic) in prehistory and history, the author's main thesis being that "When we survey the fall in each case of the great empires and creative cultures from India to the West, this much is always clearly to be seen: that every 'fall' of a people of Indo-European speech is brought about through the running dry of the blood of the creative, the Nordic race."

In the concluding chapters the author discusses the position of the Nordics at the present time—not only in Europe but in America as well—pointing out the dangers that beset this strain of the human race, which the author regards as particularly valuable.

There are numerous illustrations, which assist the reader to a better understanding of the comparisons which the author makes between the different races. The book as a whole is a piece of Nordic propaganda, reasonably sound on the somatological side, but much more dubious when it goes over into the fields of history and race psychology.

A SURVEY OF THE SOCIAL STRUCTURE OF ENGLAND AND WALES *as Illustrated by Statistics.*
By A. M. Carr-Saunders and D. Caradog Jones. *Oxford University Press*
10 shillings *London*
$5\frac{1}{2} \times 8\frac{1}{2}$; xvii + 246

An admirable attempt to recover the dry bones of social statistics with flesh, to reconstruct from the data of the Census and other statistical sources the organism called English society. Starting with an analysis of the population by age and sex the authors are led to an examination of

marital condition, family groups, housing, urbanization and geographical distribution of the population, industry, occupation, industrial status, trade unions and professional associations, political, social, and religious associations, the national income and its distribution, the national wealth, education, entrance into occupations, state provision against misfortune and its effect on the distribution of the national income, voluntary provision against misfortune, charities, poverty, crime, and the inborn qualities and recruitment of the population. The reader unversed in statistics will have a new idea when he finishes the book of how illuminating the statistical treatment of a subject may be. The discussions of official terminology are sometimes diverting. Thus the definition of a rural district as "one under a rural district council" is reminiscent of Sydney Smith's definition of an archdeacon as "a person performing archidiaconal functions." There is an appendix giving the sources of information but no index.

EPIDEMIC INFLUENZA. *A Survey. By Edwin O. Jordan.*

American Medical Assoc.
$5.00 $5\frac{3}{8} \times 8\frac{1}{2}$; 599 *Chicago*

This treatise is destined to be of great and permanent value as a document in the history of epidemiology. For it is a thorough, sound, critical and comprehensive digest of all that is known about the great pandemic of influenza which occurred with such devastating results in 1918. Probably no one was so well qualified to undertake this difficult task as Professor Jordan, both because of his wide-ranging knowledge and experience in epidemiology, and his calm and critical judgment. The book is of value not alone to the professional epidemiologist; the student of human biology in general will find in it much that is suggestive and useful to him. There is a bibliography covering 52 pages, and detailed author and subject indices.

NEGRO PROBLEMS IN CITIES. *A Study made under the direction of T. J. Woofter, Jr.*

Doubleday, Doran and Co., Inc.
$2.50 net *Garden City, N. Y.*
$5 \times 7\frac{1}{2}$; 285

The rapid increase of the negro population in American cities, from 750,000 in 1870, to 2,000,000 in 1900, and 4,000,000 in 1925, justifies a thorough survey of the environmental factors which affect the negro, and his reactions to them. This survey, made by the Institute of Social and Religious Research, gives the results of studies made in seven northern and nine southern cities. It is concerned chiefly with housing, schools, and recreations of the negro and negro neighborhoods. A staff of four people, two white and two colored, investigated conditions in these cities, and with the aid of local individuals and organizations amassed considerable pertinent information bearing upon the negro problem.

MAX VON PETTENKOFER. *His Theory of the Etiology of Cholera, Typhoid Fever and Other Intestinal Diseases. A Review of His Arguments and Evidence. By Edgar E. Hume.*

Paul B. Hoeber, Inc.
$1.50 net $5 \times 7\frac{1}{2}$; xv + 142 *New York*

Dr. Hume has done a real service to epidemiology and preventive medicine, and to human biology generally by resurrecting Pettenkofer's work from the oblivion into which it had almost com-

pletely fallen. Max von Pettenkofer was a great man, who paid a heavy penalty for having lived at the same time that Pasteur did. Even to this day it is impossible for any sort of bacteriological work relating to disease to get consideration strictly and solely on its objective merits. All such work is evaluated, consciously or unconsciously, on the basis of dicta laid down by Pasteur and Koch. Pettenkofer's theories of epidemics fared badly under such Procrustean limitations. Hume says that his hypothesis is "no longer tenable." But is there any general theory of epidemiology today which pretends that it includes all the variables which are important in the production of epidemics?

Dr. Hume has written an extremely interesting and valuable little book. There is a bibliography of 285 titles.

AUTOUR DES INSCRIPTIONS DE GLOZEL.
By René Dussaud. *Armand Colin*
5 francs $5\frac{1}{4}$ x 8; 57 (paper) *Paris*

The Glozel controversy has become the leading topic of conversation wherever anthropologists and archaeologists are gathered. The French workers in these fields are apparently irreconcilably divided on the matter. The official report, and the writings of independent investigators who have studied the *corpus delicti* on the spot, serve apparently only to widen the breach, instead of bringing the contending parties together.

In the present pamphlet the author, who is a member of the Institute, an assistant curator of the Louvre, and a specialist on Semitic inscriptions, comes to the conclusion that all the inscriptions on the famous tablets alleged to have been excavated at Glozel are fakes, pure and simple.

NATURAL MAN. *A Record from Borneo.*
By Charles Hose. *The Macmillan Co.*
\$10.00 $6\frac{1}{2}$ x $9\frac{3}{4}$; xvi + 284 *New York*

Sir Charles Hose has been for many years an administrative officer in Borneo. He collaborated with Professor William McDougall in writing *The Pagan Tribes of Borneo*, and has aided with material comparative anatomists and anthropologists all over the world. This book is based on his long personal acquaintance with the various native tribes of Borneo, and contains a wealth of material of great value to the student of cultural evolution. Of particular interest is his account of the Punans, a tribe which has practically no culture whatever. These people are, in some sense, cultural fossils, comparable in their significance for the study of cultural evolution to that of *Archaeopterx* in the study of comparative anatomy. The book is interestingly written, and well indexed. Professor Elliot Smith contributes an introduction.

MAYA CITIES. *A Record of Exploration and Adventure in Middle America.*
By Thomas Gann. *Charles Scribner's Sons*
\$5.00 $5\frac{3}{4}$ x 9; 256 *New York*

The author, who is an experienced traveller and explorer, entertainingly describes his most recent discoveries and adventures in British Honduras. Besides being of importance archeologically, the book is charmingly written. Numerous illustrations give it added interest. The author incidentally records a good many interesting and new observations on the plant and animal life of the region. Perhaps the outstanding feature of the book is the picture it gives of the still unexploited opportunities for discoveries in British Honduras regarding the Maya and earlier civilizations.

LE NON-CIVILISÉ ET NOUS. *Différence Irréductible ou Identité Foncière?*
By Raoul Allier. *Payot*
25 francs $5\frac{5}{8} \times 9$; 317 (paper) *Paris*

This is an analysis of the primitive mind, starting from the basic question as to whether there are two fundamentally different kinds of human beings—one capable of making all the progress and the other destined merely to serve the former or perish. The conclusion is that, at bottom, all human beings have a good deal in common, although some have been the victims of a knotty entanglement psychically which seems to have permanently arrested all possibility of any new development. The bearing of all this on the problem of colonization is one of the chief concerns of an interesting book.

LA FRANCE ET LES ÉTRANGERS (*Dépopulation. Immigration. Naturalisation*).
By Charles Lambert. *Librairie Delagrave*
7 francs $4\frac{3}{4} \times 7\frac{3}{8}$; 155 (paper) *Paris*

Although at bottom a piece of political propaganda, with an introduction contributed by M. Herriot, this little volume will be a useful addition to the library shelves of the human biologist interested in the problem of migration. Since the war France has had such a large immigration that the thoughtful among her citizens are beginning to be disturbed over its present and potential consequences. This book is a discussion of the facts, and of what is to be done about them.

LA QUESTION DU LAIT. *Étude Médicale, Biologique et Sociale.*
By J. Rennes. *Masson et Cie*
18 francs $6 \times 9\frac{1}{8}$; 222 (paper) *Paris*

Those in this country who have struggled to secure clean and wholesome milk will doubtless be interested in this account of the problem as it presents itself in France. The author discusses first, the factors that affect the goodness and badness of milk; second, the political and psychologic factors involved in the campaign for better conditions; and third, the psychology of the milk man and the methods to be used in teaching him and in controlling his behavior.

STAMMBAUM UND ARTBILD DER DEUTSCHEN UND IHRER VERWANDTEN. *Ein kultur- und rassengeschichtlicher Versuch.*
By Fritz Kern. *J. F. Lehmanns Verlag*
13 marks (paper) *München*
15 marks (bound)
$6 \times 8\frac{3}{4}$; viii + 305

The general conclusion of this semi-popular treatise, with 445 illustrations, which discusses the evolutionary ancestry of the German people, is that what has hitherto been regarded as the pure Nordic race is probably a composite of two races—one the descendants of Cromagnon man, the other the true Nordic race. In present day Germans are to be seen both races in close combination and more or less complete fusion.

ABRISS DER ERBBIOLOGIE UND EUGENIK.
By R. Fetscher. *Otto Salle*
4 marks $5\frac{1}{2} \times 7\frac{3}{8}$; viii + 155 *Berlin*

An excellent little popular treatise on human inheritance and eugenics, constituting Volume 10 of a series with the general title "*Mathematisch-naturwissenschaftlich-technische Bücherei.*" There are 79 illustrations, and a brief bibliography of the more important German books on the subjects treated.

RASSENKUNDE DES DEUTSCHEN VOLKES.
By Hans F. R. Günther.
J. F. Lehmanns Verlag
12 marks (paper) *München*
14 marks (bound)
$5\frac{7}{8}$ x 9; viii + 498

The twelfth edition of a popular treatise on the race biology of the German people. It is extensively and well illustrated, and on this account, chiefly, valuable as a reference book for students of human biology generally. The significance of the Nordics in the general scheme of things is not underemphasized.

THE SEARCH FOR ATLANTIS. *Excursions by a Layman Among Old Legends and New Discoveries.*
By Edwin Björkman. *Alfred A. Knopf, Inc.*
$2.00 5 x $7\frac{1}{2}$; 119 *New York*

A theory concerning Atlantis. The author, who is not primarily an archaeologist, has delved with enthusiasm into classical legends and modern archaeology and from this study has produced a book which the general reader will find of interest. He links Atlantis with the Island of Scheria, the home of Nausicaä, and also with the ancient city of Tarshish, sister city to Glades (modern Cadiz).

RASSENFORSCHUNG. *Eine Einführung in rassenkundliche Methoden.*
By Walter Scheidt. *Georg Thieme*
5.80 marks $6\frac{1}{2}$ x $9\frac{3}{4}$; 82 (paper) *Leipzig*

A useful little handbook of anthropometric technique and statistical methods, which will be particularly interesting to students of constitutional medicine, as well as to anthropologists.

MORTALITY AMONG NEGROES IN THE UNITED STATES. *Public Health Bulletin No. 174.*
By Mary Gover.
U. S. Government Printing Office
15 cents *Washington, D. C.*
$5\frac{7}{8}$ x $9\frac{1}{4}$; vi + 63 (paper)

A thorough and valuable study of the mortality statistics of negroes in comparison with whites. It will be found useful by all students of human biology.

ZOOLOGY

LES ÉLATÉRIDES DE L'INDO-CHINE FRANÇAISE.
By F. Fleutiaux.
25 francs $6\frac{3}{8}$ x 10; 71 (paper)

THERMOSBÆNA MIRABILIS MONOD. *Remarques sur sa morphologie et sa position systématique.*
By Th. Monod.
8 francs $6\frac{3}{8}$ x 10; 30 (paper)

CONTRIBUTION À L'ÉTUDE SYSTÉMATIQUE ET BIOLOGIQUE DES TERMITES DE L'INDOCHINE.
By Jean Bathellier.
80 francs $6\frac{3}{8}$ x 10; 240 (paper)

LES GALLINACÉS ET PIGEONS DE L'ANNAM.
By J. Delacour and P. Jabouille.
Société d'Éditions Géographiques, Maritimes et Coloniales
40 francs $6\frac{3}{8}$ x 10; 92 (paper) *Paris*

These four pamphlets, all published in 1927, are parts of the first volume of a noteworthy zoological enterprise, the *Faune des Colonies Françaises*, undertaken by the indicated publisher, under the general editorial direction of Professor Gruvel, and the patronage of the Colonial Ministry, the Academy of Sciences, the Pasteur Institute, and a number of other similarly important bodies.

The first fascicle noted is a purely taxonomic list of the elaterid beetles of French Indo-China.

The second discusses the morphology of the extraordinary thermophile crustacean discovered in Tunisia and described by Monod in 1924. He now shows that it is an adult form, and creates for it a new order, the Thermosbaenacea, lying between the Mysidacea and the Tanaidacea.

The third fascicle is an important contribution to the general biology of the termites, dealing successively with a systematic catalogue of the species of termites found in Indo-China; observations on their habits, habitations, means of defense, etc.; their development and the determination of castes; and finally the cultivation of mycelia by the termites of Indo-China. The treatise is extensively and well illustrated and concludes with a bibliography covering five pages.

The last of these four fascicles is a taxonomic review of the Phasianidae, Turnicidae, and Columbae of Annam, fully illustrated by text figures and plates, many of the latter being colored.

To this worthy enterprise, the *Faune des Colonies Françaises*, we wish all success.

NATURAL HISTORY: ANIMALS. TABLE OF GESTATION PERIOD AND NUMBER OF YOUNG. *An Appendix to Natural History: Animals.*
By George Jennison. *A. and C. Black, Ltd.*
12s. 6d. $5\frac{3}{4} \times 8\frac{5}{8}$; xv + 344 *London*
Appendix 1 shilling
$5\frac{1}{2} \times 8\frac{1}{4}$; 8 (paper)
(Sold in United States by The Macmillan Co., New York, $4.50)

"An Illustrated Who's Who of the Animal World" is the sub-title given to this book by the author, late Curator of the Zoological Garden at Manchester. This dictionary of mammals has obviously been compiled with much care and labor. It should prove a valuable book for identification purposes, since by its numerous illustrations and detailed descriptions easy recognition of a considerable number of genera and species is possible. There are over 300 photographic illustrations, and 16 full page illustrations in color.

The descriptions pay especial attention to size and external form. Certain special features, such as the curiously different markings of predatory and peaceful animals, the longer life of caged creatures in countries other than their own, the expectation of life of a specimen caged in good health, also many historical references culled from old pictorial or written records, have been included in this interesting book. An extensive table on gestation periods (which may be obtained separately) is appended at the end of the book.

THE PLATYPUS. *Its Discovery, Zoological Position, Form and Characteristics, Habits, Life History, etc.*
By Harry Burrell.
Angus and Robertson, Ltd.
25s. (post 6 d.) *Sydney, Australia*
$5\frac{1}{2} \times 8\frac{5}{8}$; 227

This book is the outcome of nearly twenty years personal observation of *Ornithorhynchus paradoxus* in its natural haunts, carried out while the author was engaged in collecting for the University of Sydney. It is intended mainly for the general reader, but will be an extremely valuable addition to every biological laboratory where comparative anatomy and evolution are taught. It is illustrated with 35 plates in addition to text figures. The ground covered is as follows: Dis-

covery and early descriptions; controversy on the zoological position; controversy on the laying of eggs; general characteristics; nervous organization and sensory perceptions; the spur and crural gland; the nesting-burrow; distribution and haunts; habits; breeding habits and life history; preservation and economics; the platypus in captivity. There is a bibliography covering four pages of fine print.

We heartily recommend this book to everyone interested in natural history, from any angle whatever.

ANIMAL LIFE OF THE CARLSBAD CAVERN.

By Vernon Bailey.

The Williams & Wilkins Co.

$3.00 $5\frac{1}{4} \times 8$; xiii + 195 *Baltimore*

Carlsbad Cavern, "the most extensive and spectacular cavern yet discovered in America if not in the world," in Southeastern New Mexico, was set aside as a National Monument by President Coolidge in 1923. The National Geographical Society has supported a thorough study of its geology, structure, formation and extent. To Dr. Vernon Bailey was entrusted the study of the animal life of the cavern. The present report he regards as a preliminary reconnaissance, to be followed by a more extensive work in the future. He writes chiefly of mammals, there being a paucity of invertebrate life, due largely to the lack of organic matter to serve as food for such forms. This book will be of especial interest to the naturalist, but the visitor to the caverns will do well to include it in his luggage in order to satisfy his curiosity should he develop the yearnings of a naturalist.

BIRDS AND BEASTS OF THE ROMAN ZOO. *Some observations of a Lover of Animals.*

By Th. Knottnerus-Meyer. Translated by Bernard Miall. *The Century Co.*

$4.00 $5\frac{1}{2} \times 8\frac{1}{8}$; vii + 378 *New York*

A very interesting account of the author's life-long experience with animals in zoological gardens, with particular reference to the garden in Rome, of which he is the director. Dr. Knottnerus-Meyer got his training in Germany, in the Hagenbeck tradition. The book is a mine of information for the student of animal behavior and psychology, entertainingly written and fully and well illustrated. Unfortunately there is no index.

PRÉCIS DE PARASITOLOGIE.

By E. Brumpt. *Masson et Cie*

100 francs $5\frac{3}{4} \times 7\frac{1}{2}$; viii + 1452 *Paris*

This is the fourth edition of what is generally considered to be the best book on parasitology in the French language. It contains 795 figures in the text and 5 plates, 2 of them colored. The third edition, which appeared in 1922 and consisted of 1216 pages, has been entirely rewritten. The book opens with an introduction of 54 pages on parasitism in general; this is followed by four sections, —346 pages on protozoa, 423 pages on parasitic worms, 321 pages on arthropods, and 258 pages on vegetable parasites, especially fungi. A chapter of 60 pages on the spirochaetes is included in the section on protozoa. In covering such an enormous field the author has set for himself a difficult task. He has, nevertheless, acquitted himself with credit. The subject matter is almost entirely devoted to parasites of man. Naturally the

author, who is himself a distinguished investigator in the several fields covered by the book, emphasizes his own particular views, a procedure that is not very satisfactory in a text-book. Another failing exhibited by the author is that of accepting without sufficient scepticism the results of certain other investigators, principally those of medical men who have had little or no training in parasitology. On the whole, however, the book gives an admirable survey of the subject of human parasitology.

THE PLANT LICE OR APHIDIDAE OF GREAT BRITAIN. *Vol. II.*

By Fred V. Theobald. *Headley Brothers*
30 shillings $5\frac{3}{4} \times 8\frac{3}{4}$; 411 (paper) *London*

This is the second volume of a monographic review of the Aphididae, the first volume of which was noticed earlier in these columns. This section of the work carries the discussion part way through the Tribe *Callipterini*. The descriptions are very thorough, not only in respect of morphology, but also of habits, host plants, general ecology, etc. The work when completed will be a standard reference work for a long time to come.

A SHORT ILLUSTRATED GUIDE TO THE ANOPHELINES OF TROPICAL AND SOUTH AFRICA.

By Alwen M. Evans.
University Press of Liverpool
7s. 6d. (paper) $7\frac{1}{4} \times 10\frac{1}{4}$; 79 *Liverpool*
9 shillings (cloth)

This compact but comprehensive survey of the anopheline mosquitoes of Africa south of the Sahara should be of great value to sanitary officers working in that continent. Keys for the identification of all adult anophelines and of some of the common larvae are included. Under each species the distinctive characteristics and variations of adults and larvae are briefly discussed, and the available information on habits, breeding places and pathogenicity is summarized. The ten text-figures are largely devoted to the delineation of larval details, while five beautifully executed half-tone plates present the color-patterns of wings, legs, palps, etc., very accurately and effectively. The six plates which reproduce photographs of various anopheline breeding places add little to the book and might well have been omitted.

MYSTERIES OF THE ZOO.

By Helen M. Sidebotham.
Cassell and Co., Ltd.
5 shillings net $4\frac{7}{8} \times 7\frac{1}{4}$; 192 *London*

This book gives a brief history of the birth and development of the London Zoo. In an entertaining manner are described the individual habits, the likes and dislikes and friendships of many of the famous animals that have made the Zoo one of the most fascinating places in London. The ten illustrations are well chosen.

ANIMAL ECOLOGY. *With Especial Reference to Insects.*

By Royal N. Chapman.
Burgess-Roseberry Co.
\$6.00 *Minneapolis*
$8\frac{1}{2} \times 10\frac{3}{4}$; ix + 183 (paper)

This is the second edition of an elementary textbook of animal ecology, issued in mimeograph form, and embodying a course in the ecology of insects which the author has given at the University of Minnesota for nine years. The book is characterized by two highly valuable

features; first, the quantitative method of approach to ecological problems which is emphasized throughout, and, second, the extensive bibliographies. It is to be hoped that the author will feel willing to make it more widely and comfortably available in printed form before long, for it is an excellent book.

PHYSICAL OCEANOGRAPHY OF THE GULF OF MAINE. *Bulletin of the Bureau of Fisheries Vol. XL, Part II.*
By Henry B. Bigelow.
U. S. Government Printing Office
$1.50 *Washington, D. C.*
$7\frac{1}{2}$ x 11; 516 (paper)

This volume completes a general report on the oceanographic survey of the Gulf of Maine, which has been issued in three parts. The first was devoted to fishes (Bigelow and Welsh, 1925), and the second to Plankton (Bigelow, 1926). They have been noticed in earlier numbers of The Quarterly Review of Biology. In the preparation of the final memoir, in which the various physical features are treated with great detail, the author had the collaboration of R. Parmenter and E. H. Smith. A lengthy bibliography completes the volume.

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung X.*
Edited by G. Grimpe and E. Wagler.
Akademische Verlagsgesellschaft m.b.H.
16.80 marks 6 x $8\frac{1}{2}$; 204 (paper) *Leipzig*

This number of the handbook of the fauna of the North and Baltic Seas, earlier parts of which have been noticed in these columns, contains three articles: Gastrotricha, by A. Remane; Halacaridae, by K. Viets; and Teleostei Physoclisti 11–15, by E. W. Mohr and G. Duncker.

MAMMALS AND BIRDS OF MOUNT RAINIER NATIONAL PARK.
By Walter P. Taylor and William T. Shaw.
U. S. Government Printing Office
85 cents *Washington, D. C.*
$5\frac{3}{4}$ x $9\frac{1}{8}$; viii + 249 (paper)

A handbook, prepared primarily for National Park visitors, but of much wider interest and usefulness. It should be in every zoological library as a reference work in vertebrate zoology, natural history, and ecology. The book is extensively and beautifully illustrated.

SAGITTA. *Liverpool Marine Biology Committee Memoirs on Typical British Marine Plants and Animals.*
By S. T. Burfield.
The University Press of Liverpool, Ltd.
6s. 6d. *Liverpool*
6 x $9\frac{1}{2}$; viii + 104 + 12 plates

This twenty-eighth number in the L. M. B. C. series of memoirs deals with the typical chaetognath. The morphology of *Sagitta* is described and illustrated in detail. This is followed by a short section on the embryonic development, and a bibliography of 109 titles.

BOTANY

PLANT AUTOGRAPHS AND THEIR REVELATIONS.
By Sir Jagadis Chunder Bose.
The Macmillan Co.
$2.50 $5\frac{1}{2}$ x $7\frac{3}{4}$; xvi + 240 *New York*

This is stated to be the first book that Professor Bose has ever written for the lay reader. It is a popular summary, with numerous illustrations, of the results of his varied researches. It makes fascinatingly interesting reading. Unfortu-

nately there seems to be a good deal of doubt on the part of plant physiologists, within whose field most of the work falls, as to the soundness of some of the results, and particularly some of the conclusions.

FORESTS AND WATER IN THE LIGHT OF SCIENTIFIC INVESTIGATIONS.
By Raphael Zon.
U. S. Government Printing Office
20 cents *Washington, D. C.*
$5\frac{7}{8}$ x 9; 106 (paper)

This reprint from the Report of the National Waterways Commission, in which the author has sought to assemble all the well established scientific facts in regard to the relation of forest to water supply, will be of great value to the student of these problems. The statement of what is already definitely known serves to show where future problems lie. Of especial usefulness is the bibliography covering 36 pages at the end of the paper.

THE MARINE ALGÆ OF FLORIDA WITH SPECIAL REFERENCE TO THE DRY TORTUGAS. *Papers from the Tortugas Laboratory of the Carnegie Institution of Washington. Volume XXV. Publication 379.*
By Wm. Randolph Taylor.
Carnegie Institution
\$3.00 (paper) *Washington, D. C.*
\$4.00 (cloth)
$8\frac{3}{4}$ x $11\frac{1}{4}$; 219 + 37 plates

A taxonomic treatise, thoroughly documented and illustrated, with notes on the ecological aspects of the algal flora of the Dry Tortugas.

LA SPORE DES CHAMPIGNONS SUPÉRIEURS. *Couleur. Forme. Ornementation. Terminologie. Valeur Taxonomique.*
By E. J. Gilbert. *Librairie E. le François*
20 francs $4\frac{3}{4}$ x $7\frac{1}{2}$; 221 (paper) *Paris*

This is the first volume of a proposed series *Les Livres du Mycologue.* It is a thorough discussion of the morphology of the spores of mushrooms, and their taxonomic significance. Its usefulness would have been greatly enhanced if it had been more adequately illustrated. In the whole book there is but one plate containing 14 line drawings. Except for this defect it is an excellent piece of work.

REPORT OF THE HARVARD BOTANICAL GARDENS, SOLEDAD ESTATE, CIENFUEGOS, CUBA. *(Atkins Foundation.) 1900—1926.*
By Robert M. Grey.
Harvard University Press
\$1.25 *Cambridge, Mass.*
$7\frac{5}{8}$ x $10\frac{5}{8}$; 113 (paper)

A report, covering a quarter of a century, of the Harvard Botanical Gardens at Cienfuegos. It is chiefly concerned with meteorological and phenological data, and a description of introduced and acclimatized forms.

MORPHOLOGY

ANATOMIE COMPARÉE DU CERVEAU.
By R. Anthony. *Gaston Doin et Cie*
70 francs $6\frac{1}{8}$ x $9\frac{3}{8}$; 359 (paper) *Paris*

A comparative morphological treatise, having for its aim a better understanding of the human brain. The first chapter embodies a detailed and interesting discussion of brain-weights and their significance. There then follow morphological

discussions of the telencephalon, the rhinencephalon, the neopallium, and the grey nuclei of the telencephalon. There are 234 illustrations, and an author, but no subject index. The book will form a useful addition to anatomical libraries.

ENTWICKLUNGSGESCHICHTE DES MENSCHEN *mit Berücksichtigung der Wirbeltiere.*
By L. Michaelis. *Georg Thieme*
8.70 marks *Leipzig*
5 x 7¾; viii + 253 + 4 plates

This is the tenth edition, revised and enlarged by Prof. Richard Weissenberg, of an elementary textbook of human embryology. It follows conventional lines but is brought thoroughly up to date.

PHYSIOLOGY

THE ENDOCRINES IN GENERAL MEDICINE.
By W. Langdon Brown.
Paul B. Hoeber, Inc.
$3.00 5⅜ x 8½; vii + 144 *New York*

This volume is primarily intended for the general practitioner. Based largely on the author's personal laboratory and bedside experience, the book first introduces the reader to the "biological position of the endocrine system in relation to the visceral nervous system, which seems to me to provide a key to its mode of action." Throughout the book the discussions of the physiology of the various endocrine glands are freely illustrated by the citation of clinical cases. While the chapters are necessarily brief, there is not so much condensation as to make difficult reading. The book is well indexed, but lacks any bibliography, which would seem to indicate that the author presupposes a lack of time or possibly interest on the part of his audience to follow up the subject in more technical literature. Dr. Brown sees the future of endocrinology as follows:

> As the psychological make-up depends in large part on the endocrine pattern, endocrinology will play an increasing part in the study of psychoneuroses, and in the rational determination of vocation; pharmacology will come to the aid of substitution therapy; greater use will be made of the antagonisms and coöperations between the different endocrines; and endocrinology will help in the treatment of hepatic diseases.

THE COMPARATIVE PHYSIOLOGY OF INTERNAL SECRETIONS.
By Lancelot T. Hogben.
The Macmillan Co.
$4.00 5½ x 8¼; 148 *New York*

This is a concise but critical and thorough review of the present state of knowledge regarding the physiology of the endocrine glands. The material is discussed under the following heads: Chemical co-ordination; adrenaline and neuromuscular co-ordination; internal secretion and the chromatic function; endocrine factors in secretory processes; the relation of internal secretions to vasomotor regulation; endocrine factors in metabolism; the rôle of the ductless glands in developmental processes.

The book will be of great value for reference purposes in the field of endocrinology. This being so it seems a pity that the documentation of the literature is not more comprehensive. At the end of each subject section a short list of the more important references is given, but the exact location of many of the citations in the text is difficult or impossible to find anywhere in the book. This is a matter of no great moment to the specialist in the field, who already knows the literature, but diminishes the otherwise great use-

fulness of the book to the beginning student of endocrinology.

THE GLANDS OF DESTINY. (*A Study of the Personality.*)
By Ivo Geikie Cobb. *The Macmillan Co.*
$3.00 $4\frac{3}{4}$ x $7\frac{1}{4}$; vii + 295 *New York*

This is a readable discussion of the effects produced by the glands of internal secretion on the mind and character of the individual. It is one of a number that have appeared recently, all of them designed for lay consumption. Although the author shows a commendable tendency to stick to facts the spirit of the journalist occasionally gets the better of him as on pages 82 and 83 where we learn that, "It is apparent that the individual capable of a speedy response is, in all probability, one who has an active adrenal medulla," and that "The adrenal type is a quiet, alert and successful one." To be sure his conscience bothers him a bit, and to show that he might be worse he quotes Berman to the effect that one "adrenal-centered type" is "Hairy, dark, masculinity marked, with tendency to diphtheria and hernia."

ALLGEMEINE PHYSIOLOGIE. *Handbuch der normalen und pathologischen Physiologie. Band I.*
64 marks (paper) *Julius Springer*
69.60 marks (bound) *Berlin*
$6\frac{7}{8}$ x $10\frac{1}{4}$; xii + 748

This first volume of a new, comprehensive Handbook of physiology, which is to be completed in some 17 volumes, under the general editorship of Professors Bethe, von Bergmann, Embden, and the late Prof. Ellinger, contains the following articles: Definition of life and the organism, by J. v. Uexküll; the chemical system of the organism and its energy relation, by W. Lipschitz; enzymes, by P. Rona; physical chemistry of colloid systems, by G. Ettisch; bioenergetics, by H. Zwaardemaker; irritability and stimulation, by P. Broemser; general conditions of life, by A. Pütter; interchange of material between the protoplast and its surroundings, by R. Höber; ion effects, by H. Reichel and K. Spiro; narcosis, by H. H. Meyer; protoplasmic poisons, by H. Reichel and K. Spiro; the functional significance of cell structure, particularly with reference to the nucleus, by G. Hertwig; division of labor in higher organisms, by O. Steche; parasitism and symbiosis, by O. Steche; evolution and adaptation, by J. v. Uexküll; the circulation of matter in nature, by K. Boresch. There is a subject, but no author index. The book will be a useful reference source for the general biologist.

ELEMENTS OF PHYSIOLOGY. *For Students of Medicine and Advanced Biology.*
By Ernest G. Martin and Frank W. Weymouth. *Lea and Febiger*
$8.00 net $5\frac{3}{4}$ x $9\frac{1}{4}$; 784 *Philadelphia*

The guiding ideas around which this new textbook of physiology is written are first that living protoplasm is a system of molecules and ions, hence understanding of its structure and functioning is to be sought by attempting to apply to it the physical, physico-chemical and chemical laws by which the interrelations of molecules and ions are described. The second basic idea is that every protoplasmic cell is inherently a self-sustaining system. Consequently, if it is continuously provided with a proper environment, it should continue to live and function indefinitely (subject, of course, to the possible influence of intrinsic senility).

The material is organized under the following general heads: The nature and capacities of protoplasm; cell environment; bodily maintenance; external adjustment. The book is well written, and will be found useful by all teachers of physiology.

HIPPOCRATES. *Vol. III.*
Translated by E. T. Withington.
William Heinemann Ltd.
Cloth 10s. net *London*
Leather 12s. 6d. net
$4\frac{1}{8} \times 6\frac{1}{2}$; xxvii + 455

This recent addition to the Loeb Classical Library deals with the surgical works of Hippocrates, which are in some respects the most important of his writings. The editor and translator is a private English scholar, not connected with any university, whose thorough knowledge of Greek scientific and medical writings has been utilized in the preparation of the new Liddell and Scott lexicon.

This volume will interest all biologists, as well as medical men, who are interested in the historical side of their subject. The chief thing which strikes the reader is, once more, the extraordinary modernity of the ancient Greeks.

THE HARVEY LECTURES. *1926–1927. Series XXII.*
The Williams & Wilkins Co.
\$4.00 $5\frac{1}{4} \times 8$; 164 *Baltimore*

The lectures included in this volume have the following titles: Origin and dissemination of tuberculosis according to recent investigations, by Fred Neufeld; the nature of the living cell as revealed by microdissection, by Robert Chambers; some problems concerning the gastric juice, by Leonor Michaelis; analysis of the action potential in nerve, by Joseph Erlanger; health and activity, by Edgar L. Collis; organic chemistry—its relation to medicine, by Richard Willstätter; the exchange of material between the erythrocyte and its surroundings, by Merkel H. Jacobs.

The lectures of Dr. Chambers, Dr. Willstätter, and Dr. Jacobs are of particular interest to the general biologist. Unfortunately there is no index.

QUESTIONS PHYSIOLOGIQUES D'ACTUALITÉ.
By Léon Binet. *Masson et Cie*
18 francs $6\frac{1}{4} \times 9$; 227 (paper) *Paris*

This volume contains a series of lectures and critical reviews covering a wide range of particularly lively physiological subjects. The material was presented as lectures, in what must have been an unusually interesting course inaugurated by the author, under the Faculty of Medicine at Paris, in the academic year 1925–1926. Some of the subjects discussed are: Histophysiological studies of the lung; relations between the intestine and the lung; physiological observations on mountain sickness; anticoagulants; experimental study of haemorrhage; thirst; the physiology of sleep; internal factors of growth; physiological study of tobacco smoking; etc.

THE MECHANICS OF THE DIGESTIVE TRACT. *An Introduction to Gastroenterology.*
By Walter C. Alvarez. *Paul B. Hoeber, Inc.*
\$7.50 net 6×9; xix + 447 *New York*

The second edition of a well-known and valuable treatise on the physiology and pathology of the alimentary canal. The revision and addition of material has been

so great as to make this edition practically a new book, and a reliable and authoritative digest of what is known in this branch of physiology. The book is abundantly illustrated and contains a bibliography of 900 titles. Dr. Alvarez says that this bibliography "is probably the best part of the book." With this we cannot agree. The scientific and literary skill with which this mass of raw material has been analyzed and integrated by Dr. Alvarez is a contribution of first rate importance.

LIVING MACHINERY.

By A. V. Hill. *Harcourt, Brace and Co.*
$3.50 5½ x 8¼; xxi + 306 *New York*

This volume of Lowell lectures, by the distinguished Nobel laureate in physiology, is an extremely interesting, well-written, popular exposition of the present status of knowledge of nerve-muscle physiology. At least the first six lectures are such, being essentially a repetition of the author's Christmas lectures at the Royal Institution in London. The last two are more philosophical in character and deal respectively with the position of physiology among the sciences, and a critical discussion of mechanism and teleology. The whole makes excellent reading for everyone, biologist or layman.

NUTRITION AND DIET IN HEALTH AND DISEASE.

By James S. McLester.
W. B. Saunders Co.
$8.00 6 x 9½; 783 *Philadelphia*

This treatise on nutrition is written particularly for the medical man. Nearly two-thirds of the book is devoted to the discussion of nutrition in disease. A great deal of attention is given to dietaries supposed to be particularly suited to various diseased conditions. The interest of the book is therefore rather special than general, but it accomplishes very well the task set. Practising physicians will find it useful as a comprehensive reference work.

THERMIONIC PHENOMENA.

By Eugène Bloch. Translated by J. R. Clarke. *E. P. Dutton and Co.*
$2.50 4¾ x 7¼; x + 145 *New York*

This volume will be of particular interest only to the worker in the field of biophysics. Bringing together the important advances made in knowledge concerning emissions from heated bodies the author shows where confusion in this subject still exists and where there is need for the concentrated attack of investigators. A short chapter giving an account of some of the applications of thermionic phenomena, and author and subject indices add to the value of the treatise.

PRINCIPES DE PHARMACODYNAMIE.

Constitutions Chimiques; Propriétés Physiologiques.
By L. Hugounenq and G. Florence.
Masson et Cie
40 francs *Paris*
6¼ x 9; viii + 391 (paper)

A systematic treatise on pharmacology approached from the point of view of correlating chemical structure and physiological effect. The book opens with an excellent historical account of research in this field. It is extensively and internationally documented.

BIOCHEMISTRY

PHYSICAL CHEMISTRY AND BIOPHYSICS.
By Matthew Steel.
John Wiley and Sons, Inc.
$4.00 $5\frac{3}{4}$ x 9; x + 372 *New York*

A textbook in which the rudiments of physical chemistry are treated in a manner especially adapted to the requirements of medical and biological students. It is so arranged as to make it suitable for a course continuing through at least a third of an academic year. The illustrations of the application of physico-chemical principles are taken from the fields of biology, physiology and medicine. Considerable attention is given to the nature and structure of matter, while in the chapter on the Colloidal State of Matter the work of Jacques Loeb on proteins is treated with considerable detail. A number of illustrations and a complete author and subject index increase the usefulness of the book.

ÜBER DIE KATALYTISCHEN WIRKUNGEN DER LEBENDIGEN SUBSTANZ. *Arbeiten aus dem Kaiser Wilhelm-Institut für Biologie, Berlin-Dahlem.*
Edited by Otto Warburg. *Julius Springer*
36 marks (paper) *Berlin*
37.80 marks (bound)
$6\frac{1}{2}$ x $9\frac{1}{2}$; vi + 528

A collection of papers by Warburg and his students, arranged under three general heads: Respiration and fermentation; carbonic acid and nitrate assimilation; and the catalytic action of growing cells. There is appended a bibliography covering four pages, but unfortunately there is no index, which diminishes the usefulness of a compilation of separate studies like this. It is, however, a real service to have available in one volume all these scattered papers giving the results of the very important work that Dr. Warburg is doing on cellular metabolism and the cancer problem.

DIE BESTIMMUNG DER WASSERSTOFFIONENKONZENTRATION VON FLÜSSIGKEITEN. *Ein Lehrbuch der Theorie und Praxis der Wasserstoffzahlmessungen in elementarer Darstellung für Chemiker, Biologen und Mediziner.*
Dr. Ernst Mislowitzer. *Julius Springer*
Paper: 24 marks *Berlin*
Bound: 25.50 marks
$6\frac{1}{4}$ x $9\frac{1}{2}$; x + 378

The introduction by Professor Rona states that this book was prepared at his suggestion to fill a gap in the German literature occasioned by the fact that the first edition of Michaelis' treatise on hydrogen ion concentration, "ein Meisterwerk didaktischer Kunst," has for many years been out of print. The scope of the present work is sufficiently indicated in its title. There is a bibliography covering some 32 pages.

DIE METHODIK DER FERMENTE. *Lieferung I.*
Edited by Carl Oppenheimer and Ludwig Pincussen. *Georg Thieme*
28 marks *Leipzig*
$7\frac{5}{8}$ x $10\frac{5}{8}$; x + 320 (paper)

This is the first part of what is to be a large collective reference work on enzymes. It contains 20 chapters, of varying lengths, contributed by a number of different authorities in this field. The volume is divided into two parts, of which the first deals with the general methodology of enzyme investigations, physical, physico-chemical, and chemical. The

second part deals with the substrates upon which enzymes act. The whole treatise, when completed, promises to be an extremely useful reference work for biologists.

INVESTIGATIONS ON CHLOROPHYLL. *Methods and Results.*
By Richard Willstätter and Arthur Stoll. Authorized English Translation from the German by Frank M. Schertz and Albert R. Merz. *Frank Schertz*
1305 Farragut St., N.W., Washington, D.C.
$4.50 6 x 9; xii + 385 + 11 plates

The translators have performed a real public service to American and English biologists in publishing this English translation of the fundamental researches of Willstätter and Stoll on chlorophyll. Since they have published the book at their own expense and risk it is to be hoped that American biologists will indicate their appreciation by buying it for their laboratories and libraries. The translation is very well done.

L'URÉE (*Recherches de chimie analytique, biologique et agricole*). LES FONCTIONS. *Dinaphtopyranol, Xanthydrol et Sel de Pyryle* (*Chimie organique*).
By Richard Fosse.
Les Presses Universitaires de France
50 francs 6 x 9½; xii + 303 *Paris*

This is one of a series of monographs on biologic problems. Fosse is the discoverer of the xanthydrol reaction for urea. In this volume he summarizes his studies on ureogenesis and the distribution of urea in various animals and plants. As he rarely touches on the work of others, this volume can hardly be compared with the monographs of Werner and Fearom.

LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE. *II. Band. V. Lieferung.*
By Otto Fürth. *F. C. W. Vogel*
15 marks *Leipzig*
7 x 10; v + 185 (paper)

Another section of the Fürth textbook, earlier parts of which have been noticed in these columns. The present section deals with the metabolism of purins and carbohydrates generally, including at the end a chapter on lactic acid, as the most important intermediate product in the breaking down of sugar.

KURZES LEHRBUCH DER PHYSIOLOGISCHEN CHEMIE.
By Paul Hári. *Julius Springer*
18 marks (paper) *Berlin*
19.50 marks (bound)
6½ x 8½; xii + 407

The third editon of a standard text. Considerable additions have been made to bring the book up to date, and the material has been rearranged somewhat for pedagogical reasons.

SEX

SEXUAL APATHY AND COLDNESS IN WOMEN.
By Walter M. Gallichan.
T. Werner Laurie, Ltd.
7s. 6d. 4⅞ x 7⅜; 183 *London*

Another volume for the benefit of the sexually unsatisfied. In our attempt to bolster up our present civilized mode of living has it not been overlooked that through countless ages past there is no evidence that man had any more sex problems than a guineapig has? Substantially down until the Puritans saddled the west-

ern world with their dour philosophy the only books about *It* were humorous ones. This is a sound attitude, as Dr. Clendening has lately emphasized. So far as may be judged from historical and general literature, sexual apathy and coldness is a modern phenomenon. Mr. Gallichan says the usual things about its being due to inadequate education of girls in sex matters, to lack of understanding on the part of men, to the complexity of modern life, etc. We have looked in vain for anything in the way of an original note in the book.

BESTIMMUNG, VERERBUNG UND VERTEILUNG DES GESCHLECHTES BEI DEN HÖHEREN PFLANZEN. *Handbuch der Vererbungswissenschaft. Band II. Lieferung 3 (II, C.).*
By C. Correns. *Gebrüder Borntraeger*
19.20 marks *Berlin*
7 x 10½; iii + 138 (paper)

This section of the Baur-Hartmann handbook of genetics deals with the problem of sex in plants, by the foremost living authority in this field. It maintains the high standard set by the other parts of this great undertaking which have so far appeared. There is a bibliography covering nine pages.

CONTRACEPTION (*Birth Control*). *Its Theory, History and Practice (second edition). By Marie Carmichael Stopes.*
John Bale, Sons and Danielsson, Ltd.
25 shillings *London*
5½ x 8½; xxvi + 480

This new edition of Dr. Marie Stopes' *vade-mecum* for newlyweds still embodies all the author's well-known enthusiasm for more and better sex life in the home. In fact the book is not basically altered from the first issue. About 60 pages of new material have been added, but the growth between the first and second editions has been intersusceptive. The book cannot legally be imported into this land, quaintly said to be "of the free." Reginald, the Office Boy, says he found our copy on the doorstep one morning.

PSYCHOLOGY AND BEHAVIOR

SPEECH. *Its Function and Development. By Grace Andrus de Laguna.*
Yale University Press
$5.00 *New Haven, Conn.*
5½ x 8¾; xii + 363

A thorough-going attempt at a reasonable solution of an extremely difficult and complex problem, the origin of speech. The first part of the book is devoted to the development of the thesis that speech began when man's ancestors came down from the trees and began to hunt on the ground. Its origin was in the animal cry "in order to meet the demands of expanding group life."

> The evolution of language, marked by the differentiation of the proclamation, which prepares but does not precipitate response, and of the supplementary command, with its power to initiate and control particular acts, is an essential condition for the complex and varied coöperation that is involved in human hunting.

The second part of the book attempts to trace the evolution of thought which paralleled that of speech. A theory of the origin and development of the naming of objects is developed. The third part of the book recapitulates the preceding arguments from the objective point of view.

The book is a valuable contribution to the literature of human biology.

AN EXPERIMENT WITH TIME.
By J. W. Dunne. *The Macmillan Co.*
\$2.50 $5\frac{1}{2} \times 8\frac{5}{8}$; 208 *New York*

This is an interesting, if not entirely convincing, attempt to show that man's mind is capable of the correct anticipation of future events in the phenomenal world, as a definite and regular thing in contrast to a merely accidental coincidence. The book starts with an account of the author's dreams, and ends with a new theory of the universe. It thus traverses a good deal of ground. The pathway gets very obscure at times, and we fancy that most readers will have a good deal of difficulty in following Mr. Dunne all the way. But the facts which he records are extraordinary, and cannot be accounted for by any other theory at the moment. So on this account, if no other, Mr. Dunne's theory deserves respectful consideration.

STAMMERING. *A Psychoanalytic Interpretation.*
By Isador H. Coriat.
Nervous and Mental Disease Publishing Co.
\$2.00 6×9; viii + 68 *New York*

The author is of the opinion that "stammering is one of the severest forms of the psychoneuroses and is not merely a tic, an obsession, an auditory amnesia, a spasm of coördination of the muscles involved in speech, neither is it produced by a conflict of languages, according to the usual superficial interpretations of its pathogenesis. It is preëminently what may be termed an 'oral neurosis.' "

This thesis is supported by psychoanalytic arguments.

Excessive mouth erotism is, therefore, the basis of stammering, a projection from the unconscious of the precipitated components of the oral stage of libido development. The mouth has become the principal and all-powerful organ of libidinal pleasure, which is gratified, although against resistance, by the oral discharge of speech. In several instances there was noted, in addition to the frequent sucking movements with the lips and excessive salivation during the paroxysm of stammering, deep breathing, rapid heart beat, perspiration, yawning; this was followed by a feeling of relaxation after enunciation of a difficult word. Here there could be observed an actual reproduction, in adult life, of the relationship of the infant to the nipple, a gratification of the oral-erotic zone in pleasure sucking reënacted in maturity. The original attachment of the sexual excitation to the nutritional instinct, that is, the oral phase of the libido, still dominates the adult stammerer, in fact, the persistence of this phase into maturity, produces stammering in order to satisfy a compulsive-repetition, which resembles a tic.

A stutterer will never seem the same to us after this!

A STUDY OF NATIO-RACIAL MENTAL DIFFERENCES. *Genetic Psychology Monographs Vol. 1, Nos. 3 and 4.*
By Nathaniel D. Mttron Hirsch.
Clark University
\$3.00 (paper) *Worcester, Mass.*
\$3.50 (cloth) $5\frac{3}{4} \times 9$; 168

In this monograph the author gives a report of his study on the mental capacity of some of the nationalities to be found in the American population. The subjects were school children, American born, both of whose parents were foreign born and of the same nationality. Two other groups were included in the study—white American children and a group of Afro-American children. The author first gives a brief summary of some of the results and conclusions of other studies upon racial and national psychological differences; then follow chapters in which the tests given the children are described in detail, and the results analyzed. The highest testing children were Polish Jews. The last three

chapters are devoted to an hypothesis which is deemed a fair and proper interpretation of the data collected.

The author believes that intelligent action can lead to the blending of certain sub-races in the American population which would result in a desirable variability in the new stock and that such blending would produce many great men and geniuses. "An American art, drama, music and especially a new religion would arise as the creations of the genius of the new Natio-Race."

MY HAPPY CHIMPANZEE. *The Adventures of Mary, the Wonderful Chimpanzee, at the Seaside.*
By Cherry Kearton. *J. W. Arrowsmith, Ltd.*
5 shillings $5\frac{1}{2} \times 7\frac{1}{8}$; 124 *London*

This little book, while perhaps not quite so appealing to the lover of animals as the author's earlier book, "My Friend Toto," consists of another series of interesting and amusing anecdotes about the very human behavior of an almost human creature.

DE L'EXPLICATION DANS LES SCIENCES.
By Émile Meyerson. *Payot*
60 francs $5\frac{1}{2} \times 9$; 784 (paper) *Paris*

A philosophical treatise on the theory of knowledge of first rate significance to all scientific men, and especially biologists. Apart from the stimulating qualities of the author's own particular brand of monism, the work is valuable as a history of scientific ideas and methodology.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

PROPHYLAXIE ANTIVÉNÉRIENNE INDIVIDUELLE À TRAVERS LES AGES. *Essai historique.*
By E. L. A. Baude.
Librairie E. le François
6 francs $6\frac{1}{4} \times 9\frac{3}{4}$; 47 (paper) *Paris*

This is an entertaining historical account of one aspect of man's struggle with a difficult general problem, namely, how to have one's cake and eat it too. Anaxitoteles made the sage remark that the worship of no goddess is pleasanter than that of Venus. But the consequences are all too often depressing, not to say disastrous. Dr. Baude says that personal prophylaxis against venereal disease was first put on a really scientific basis by Metchnikoff in 1906. Before that time the matter had been either in the hands of quacks or of honest but stupid physicians who thought they were getting results but weren't.

This scholarly treatise of Dr. Baude's, with its bibliography of 79 titles, will form the material for a learned footnote in that *magnum opus*, in elephant folio, *The Natural History of Copulation*, to the preparation of which certain distinguished biologists propose to devote the declining years of their lives.

A BOOK OF FOOD.
By P. Morton Shand.
Alfred A. Knopf, Inc.
$4.00 $5\frac{1}{2} \times 8$; 319 *New York*

Although not a cook book this volume is about food in the home. In the preface the author says that his remarks "are addressed not merely to gourmets, to all curious and adventurous spirits in the domain of gastrosophy, but also to

malcontents with the food we eat in England today; and to men, rather than to women, among my long-suffering compatriots."

One might venture to suggest that this volume be read shortly before meal time. Not that the book is only readable under such conditions. Far from it! But, like an *Amer Picon*, a slightly famished state will whet the reader's perceptions, and along with the author his enthusiasms for *oeufs-au-plat* and *Sole à la Meunière* will carry him to happy realms. American women, whose customary source of food lore is that of the monthly magazine or daily paper, should find this book a welcome diversion.

THE IMPORTANCE OF BEING HISTORICALLY MINDED.
By Wm. Allen Pusey.

American Medical Assoc. Press
$4\frac{7}{8}$ x $6\frac{3}{4}$; 22 *Chicago*

An amusing and at the same time penetrating little tract on the present status of medicine, philosophically considered. The author is a wise old clinician, and in this address gives the brash young laboratory boys, whose behavior indicates that they suppose scientific medicine began about a fortnight after they got started, a good deal to think about. It is an excellent piece of debunkification, a word that the office cat brought in the other day.

Vol. III, No. 4 December, 1928

THE QUARTERLY REVIEW of BIOLOGY

THE CHLOROPLAST PIGMENTS, THEIR FUNCTIONS, AND THE PROBABLE RELATION OF CHLOROPHYLL TO THE VITAMINES

By F. M. SCHERTZ

Soil-Fertility Investigations, United States Department of Agriculture

INTRODUCTION

The present paper has been written to show that by a long slow process we have come to know something about the real nature of the chloroplast pigments. Carotin and xanthophyll, being the easiest to obtain, have been worked on most, yet chlorophyll has always received considerable attention. The latter has been obtained only in solution until within the past few years. All of the four chloroplast pigments have been obtained in the pure chemical state, and their probable chemical formulae have been determined. As yet little is known about the function of any of these pigments in plant metabolism. The indirect evidence submitted seems to show that chlorophyll in nature is being broken down continually to form numerous compounds. It should require no great stretch of the imagination to see that vitamines may be formed directly from chlorophyll, with which they are so intimately associated.

THE CAROTINOIDS. EVOLUTION OF IDEAS CONCERNING THE TWO CAROTINOIDS

The evolution of the names of the pigments shows us how misleading the names given to the carotin pigments have often been. Many names at times have been proposed for what now is obviously the same pigment. Botanists, chemists, and plant physiologists each evidently chose names suitable to them for the pigments which were being investigated. A diversity in nomenclature is found especially in the yellow animal pigments and can be traced in most instances to slight variations in certain of the simple properties which were regarded as specific for the various types of pigments.

Often the variations were due to the fact that the method employed for the isolation of the pigment did not insure its freedom from other pigments of similar but not identical properties. Often the pigment was examined in an amorphous condition or in solution, without reference to

the possible effect which these states might exert upon the particular properties being studied. Perhaps more often there was a contamination with lipoid impurities, which invariably accompany the pigments when they are being separated from the plant or animal tissues. Not knowing much about the chemical nature of the pigment with which he was working, very often the investigator failed to protect the pigments from high temperature and from oxidation. The earlier investigators did not realize that some of the most characteristic properties of the pigments they were working with were subject to modification even in the earlier stages of oxidation. Often the sole basis for classification of the animal chromolipoids has been certain color reactions with reagents and the spectroscopic properties of the pigment involved. These tests are now known to be insufficient for a proper classification of the yellow pigments found in plants and animals. The greatest confusion has been in the terminology of the animal pigments, but those who have been studying the pigments of plants have often proposed names already in use for pigments of obviously different composition and properties. It appears as if there is still some confusion regarding xanthophyll. Efforts at bringing order out of such a chaotic condition should be welcomed by all who are interested in our knowledge concerning the yellow pigments whether they are found in plants or animals. The efforts of Thudichum, Krukenberg, Schrötter-Kristelli, Zopf and Tswett will here be reviewed.

Thudichum (1869) was perhaps the first one to attempt to bring the various yellow pigments together under one name —"luteine" or luteins. Prior to this (1866) Piccolo and Lieben had crystallized the corpus luteum pigment and had called it luteohematoidin or hemolutein. Holm (1867) isolated the corpus luteum pigment and called it hematoidin. The luteins which Thudichum mentioned included the corpus luteum pigment, the yellow pigment of blood serum, adipose tissue and butter, and the yellow pigment of egg yolk. The vegetable pigments in the lutein group included the pigment of yellow corn, the pigment of anatto seed, pigments of the carrot root and of yellow leaves and the pigments present in the stamens and petals of many flowers. Thudichum's classification was never widely adopted.

Krukenberg (1886) proposed the name lipochrome for all the animal and plant pigments which had previously been known as luteins, carotins, zoonerythrin, tetronerythrin, chlorophan, xanthophan and rhodophan. The name lipochrome has been quite widely adopted, probably owing to the fact that the pigments were associated with fat in their natural state. Kohl (1902), however, objected to calling carotin a lipochrome, for it is known to occur in numerous cases quite free from fat.

A few years later, Schrötter-Kristelli (1895) proposed to group together all the plant and animal coloring matters which had previously been known as etiolin, chlorophyll yellow, xanthin, anthoxanthin, lutein, xanthophyll, chrysophyll, carotin, phylloxanthin, phycoxanthin, erythrophyll, solanorubin, lipoxanthin, hematochrom, chlororufin, bacteriopurpurin, hemolutein, vitellorubin, and tetronerythrin. These pigments he regarded as an homologous group, if not completely identical, and chose the name lipoxanthin as a general designation. The lipoxanthins are a more or less indefinite group of pigments, which may be classified just as well under one head by the older term

lipochrome; this is probably the reason why the proposed term was never widely used.

Zopf (1895) used the term carotin synonymously with lipochrome in most of his extensive studies of pigments of the lower forms of plants and animals. He proposed to distinguish between two groups of carotins, namely, eucarotins (true carotins), which were hydrocarbon in nature, and carotinins, which contained oxygen as well. It appears that the carotins are not related to the oxygen-containing xanthophyll which we know at the present time. Tswett (1911) proposed the name "Carotinoide" for the various chromolipoids which are chemically and generically related to carotin. He designated as carotins all those chromolipoids whose constitution and properties show them to be hydrocarbons and as xanthophylls all those whose constitution and properties show them to be oxyhydrocarbons and which are chemically as well as generically related to carotin. The terminology of Tswett has been quite widely adopted and is the one which Palmer has used in his monograph on the carotinoids. The monograph shows the chemical and physiological relation of the carotinoids to the yellow animal chromolipoids of the tissues and fluids of the higher mammals and man and of the egg yolk and bodies of oviparous animals and is probably a criterion of similar relations which extend throughout the entire animal kingdom.

Carotin as obtained from the carrot root was first described by Wachenroder (1826) one hundred years ago. He called the pigment carotin, the same name that we use. Vauquelin and Bouchardat (1830) next studied it. Zeise (1847) first isolated it in quantity sufficient for analysis and also learned much regarding its chemical properties. His analysis showed that it contained only carbon and hydrogen but its hydrocarbon nature was not definitely established until Arnaud (1886) made his careful analysis. Kohl (1902) has given us the most detailed descriptions of the chemical and physical properties of carotin, but his chemical analyses were quite unsatisfactory. Later Willstätter and Mieg (1907) definitely settled the chemical composition of carrot carotin when they proved it to be identical with the carotin of the chloroplast. It was given by them the formula $C_{40}H_{56}$, which has been generally assumed to be correct. Escher (1909) and Willstätter and Escher (1910) have completely confirmed these results. Escher perhaps is the only investigator on record who has attempted to unravel the structure of carotin. His attempts led only to the production of amorphous products; consequently its constitution still remains to be determined.

It was Fremy (1860) who first showed that a yellow pigment can be obtained from green leaves. He did this by allowing strong hydrochloric acid and ether to act upon the residues from the alcoholic extract of green leaves, or by a similar treatment of the precipitate thrown down from the alcoholic leaf extract by aluminum hydroxide. In this procedure the ether assumed a yellow color while the acid layer became bluish. Fremy called the yellow color phylloxanthine and the blue pigment phyllocyanine. Stokes (1864) first expressed the view that the phylloxanthine was a mixture of some of the natural carotinoids of the leaf with an acid decomposition product of chlorophyll. It was possibly Fremy who succeeded in obtaining for the first time crystals of carotin and perhaps those of xanthophyll from green plants. Stokes (1864) is credited with first discovering a method for actually separating the yellow pigments accompanying chlorophyll; he recognized the existence of distinct green

and yellow constituents in the plastids. Kraus (1872) is given the credit for actually first making a separation of the green and yellow chloroplast pigments. Sorby (1873) claimed that he found two green pigments and five members of the yellow pigments. Tschirch (1887) considered the yellow constituents of the chloroplast to consist of erythrophyll and a group of five xanthophylls. Besides carotin Schunck (1903) thought that the yellow pigments consisted of L, B and Y xanthophyll. Kohl (1902) attempted to harmonize the views of Tschirch and Schunck as well as his own beliefs. He believed that carotin and only two xanthophylls comprised the yellow pigments of the chloroplast.

Monteverde (1893) found that the yellow pigments accompanying chlorophyll could be divided into two groups according to their relative solubility in alcohol and petroleum ether and was the first to show that this fact offered a very simple means of separating the pigments from each other. Monteverde and later Reinke (1885) attempted to obtain crystals of the pigments. There is considerable doubt as to the exact nature of the crystals which they obtained. Tswett (1906) by this chromatographic method of analysis, using petroleum ether or carbon disulphide solutions of the chloroplast pigments, has shown that at least three and possibly four xanthophylls accompany carotin. He has characterized these pigments at great length and has written much regarding them. It was not until Willstätter and Mieg (1907) isolated the first crystalline xanthophyll and analyzed it that much has been known regarding the real nature of the xanthophylls. Xanthophyll was shown by them to probably have the formula $C_{40}H_{56}O_2$. To the writer's knowledge nobody has ever confirmed this analysis nor has its accuracy ever been questioned by anybody. Tswett (1910) has expressed the opinion that the xanthophyll crystallized by Willstätter and Mieg was a mixture of two or three xanthophylls in which his xanthophyll a predominated. Willstätter and Page (1914) later state that oxidation appears to explain the statements of Tswett regarding his different xanthophylls. Willstätter and Stoll (1913) admit that their xanthophyll might be a mixture of xanthophylls but at the same time they regard the different bands found in the chromatogram as being due to oxidation products of the carotinoids. It seems necessary that those who support statements asserting the presence of more than one xanthophyll should sooner or later furnish better proof than that existing in the literature. Final proof will be the crystallization or chemical preparation of more than one xanthophyll.

Evidence obtained by the writer has shown that some of the bands in Tswett's chromatogram are undoubtedly due to the oxidation of carotin and of xanthophyll, for when the pigments are pure and allowed to oxidize these bands appear. Spectrophotometrical data obtained at the Bureau of Standards also support the contention that there are only two yellow pigments. Only last year genetical evidence was submitted which shows that there are two sorts of carotinoid pigments in maize. One is related to the green pigments in physiological development, while the other is not thus related. All of the evidence available seems to support the contention that there are only two yellow chloroplast pigments, namely, carotin and xanthophyll, and that the other xanthophylls found in the literature are simply oxidation products of these two pigments.

OCCURRENCE OF CAROTIN AND XANTHOPHYLL IN PLANTS AND ANIMALS

Our attention will now be turned to the occurrence of these pigments in the plant and animal kingdoms. In the plant kingdom carotinoids are to be found in all of the plants which contain chlorophyll. In many cases the pigments have not been extracted and isolated but the evidence for their presence is so great that the fact cannot be denied. From the smallest algae to the mightiest tree the carotinoids are always present with chlorophyll. The flagellates too unquestionably contain these pigments, and they are even believed to occur in some of the fungi. In general, very little is known regarding their presence in bacteria, though certain species contain them.

Evidence has been collected and presented by Palmer which shows that the carotinoid pigments are widely distributed in the vertebrates and in the invertebrates. The yellow to orange-red animal pigments which have been most commonly called lipochromes are in all probability true or modified plant carotinoids. In some species both of the higher and of the lower animals it is certain that the lipochromes are true carotinoids, and it does not require a very great stretch of the imagination to fill in the gaps. In fact the presence of carotinoids in the animal kingdom is much more common than those who are not acquainted with the subject would be led to believe. It would be very interesting to list here all of the animals in which the carotinoids have been found, but for the purpose of this paper such a list is not necessary. It will suffice to mention only an example of each of the carotinoids.

In 1882 Kuhne first observed crystals of the egg yolk pigments and decided that these crystals were not identical with those found in the corpus luteum of the cow. Willstätter and Escher (1912) isolated the egg yolk pigment in sufficient quantity for a chemical analysis. They raised no query in their minds as to its possible origin from plant carotinoids. Escher's work shows very clearly that he saw no biological relationship between the xanthophyll of the egg yolk and plant xanthophyll, for he expressed the view that "the oxygen-containing luteum in the yolk of eggs plays the part of an atavistic plant respiratory pigment for the formation of hemoglobin in the embryo." The chemical and physical properties of the egg yolk pigment leave no doubt as to its identity with the plant xanthophyll which was isolated by Willstätter and Mieg (1907). In 1913 Escher definitely established the chemical identity of the corpus luteum pigment (of the cow) with plant carotin. A possible chemical relationship between certain animal chromolipoids and plant carotin was recognized by several workers before this time. On the other hand, many other workers saw no evidence of a biological relationship between plant and animal carotinoids. Paulton (1893) has shown conclusively that the color of caterpillars is largely due to the plant pigments derived from the food. In fact, it is now generally believed that all phytophagous insects derive their lipochromes and chlorophyll-like pigments from their food. The work of Palmer and his coworkers leaves no doubt in the minds of students of the carotinoid pigments that the carotin of butter fat, adipose tissue, blood serum, skin secretions, etc., of the cow is biologically derived from the food and that a similar relationship exists between the xanthophyll of egg yolk and fowl tissues and plant xanthophyll. The view has now become quite prevalent that all animal chromolipoids are derived from the carotinoids of the food and, either unchanged

or slightly modified, are the cause of the yellow to red chromolipoid colors of all species of animals.

FUNCTION OF THE CAROTINOIDS

This review of the carotinoid pigments would not be complete without discussing briefly their function in living organisms. Many views have been held regarding these pigments.

IN PLANTS

Engelmann (1887) and Kohl believed that carotin shares with chlorophyll the work of carbon dioxide assimilation and that this lies chiefly in its energetic absorption of a large part of the blue violet rays of sunlight. The spectroscopic properties of the carotinoids are one of the strongest arguments in favor of the view that they perform some definite function in the plant. Went (1904) thinks that they may serve the purpose of protecting the cell enzymes against the destructive action of certain light rays. Kohl (1900) and Arnaud have suggested that carotin may act in a respiratory rôle through its power to absorb oxygen. Willstätter and Stoll suppose that carbon dioxide assimilation is controlled by an equilibrium between the chlorophyll components a and b and that this equilibrium is in turn controlled by the carotinoids. Willstätter and Mieg on the other hand thought that carotinoids might help regulate the oxygen pressure in plant cells through their great affinity for this element. Ewart (1915) has attempted to show that carotin and xanthophyll can play a part in photosynthesis. His work, however, has been seriously questioned. Up to the present time very little study has been made of the physiological conditions which govern the formation of the carotinoids in plants or to the problem of the relations between the different carotinoids or between the carotinoids and the other plant constituents. In ripening tomatoes, carotin and lycopin formation is coincident with the destruction of chlorophyll, but there is no chemical basis for assuming that this indicates that the carotinoids are actually derived from chlorophyll. Duggar (1913) has found that the formation of the carotinoids in ripening tomatoes may be correlated with temperature. The synthesis of lycopin he found was independent of light but was dependent upon oxygen. In cases of oxygen exclusion the fruit failed to redden, even at a favorable temperature.

IN ANIMALS

In the case of animals all of the evidence presentable argues against the carotinoids performing any general physiological function. Attempts have been and are still being made to correlate the carotinoids with the vitamines but as yet no success has been obtained. There appears, however, to be a fairly definite correlation between the occurrence of carotinoids and vitamine A in plant tissues but not in animal tissues or in animal fats.

In the above discussion the writer has attempted to review the present state of our knowledge of the carotinoid pigments. An effort has also been made to indicate the long slow evolution of our knowledge of these pigments and to show that much effort has been put forth by a great many workers to establish our present conceptions regarding the chemical nature and the number of the carotinoid pigments. Perhaps at the present time information regarding the complex chemical structure of the pigments will do much to solve many of the perplexing problems. Until the chemical structure of these pigments is fully worked out there will probably be much speculation regarding their real nature in plant economy.

CHLOROPHYLL

A review of our knowledge concerning chlorophyll will now be given to show what the various workers have discovered regarding this pigment, which is so prominent in the plant kingdom. Maybe by reassembling our knowledge a new view may be gained which may prove of value to those who are not directly interested in the green pigments. The history of our ideas concerning the chloroplasts will first be reviewed.

THE CHLOROPLASTS

Comparetti was perhaps the first person to mention the green granules which we now call chloroplasts. Apparently he saw also the grains of starch which are enveloped by the green material, though he never guessed what they actually were. Sprengel, Treviranus and later Turpin believed that these green granules were really vesicles which gave birth to new cells. Moldenhauer believed that the grains of chlorophyll were derived from the coagulation of the green sap of the cells. Later Treviranus stated that the structure of the chloroplast consists of an albuminous globule with which the green material is mixed. Dutrochet considered the small green grains in the cells at the base of the petiole as equivalent to the nerve corpuscles in animals.

Mulder thought that a grain of chlorophyll could bring about the metamorphosis of a grain of starch with the sole help of the nitrogen material dissolved in the cell. Von Mohl recognized that chlorophyll occurs sometimes in irregular masses and sometimes in definitely formed grains, which may show one or more starch grains surrounded by a green jelly. Nägeli opposed the view of von Mohl that the chlorophyll grains are composed of a nucleus of one or more starch grains, surrounded by a layer of chlorophyll. Nägeli held that the chlorophyll grain is a vesicle and should be classed with the other colored globules in the cell sap. These green and colorless vesicles he assumed were analogous to cells and held that the cell is built up of these vesicles just as an organism is built of cells. Nägeli later modified his views and considered chlorophyll grains as vesicles with the green color restricted to the surface and each one bound by a cellulose membrane. He considered them to be composed of a protein substance whose surface is covered by a condensation membrane formed by contact of the grain itself with the cell sap. Von Mohl altered his original conception and recognized that although starch and chlorophyll are often found together they nevertheless arise independently.

Sachs found that chlorophyll is always united to definite portions of the protoplast. The amount of pigment is relatively very small, for its removal affects neither the shape nor the volume of the ground substance, which is always a solid, soft body containing extremely small vacuoles in which the chlorophyll is generally uniformly distributed. The chloroplasts are always imbedded in the cytoplasm and are never in contact with the vacuole or the cell wall. With few exceptions starch grains arise in the homogeneous solid substance of the chloroplasts. Sometimes drops of oil form in the chloroplast. Hofmeister developed his views further and held that the chlorophyll grain is composed of two layers, the peripheral layer being denser than the inner one.

Briosi was the first to recognize oil droplets in the chloroplasts of a pathological condition. In some plants oil forms instead of starch, and the oil exists in finely divided particles between

the "protoplasmic molecules" of the chloroplasts. Mikosch held that grains of starch could transform themselves into chlorophyll granules and Stohr also noted that the formation of the grains of chlorophyll was often preceded by the formation of grains of starch.

Frommann held that the whole plastid was composed of a fundamental network of green threads. It was Pfeffer who first showed that the plastid could not carry on photosynthesis in the absence of the chlorophyll which it normally contains. Pringsheim came to the conclusion that the ground substance of the chloroplast is a hollow sphere possessing a spongy structure and that it holds the green coloring matter in its meshes. He thought that the green pigment was only mechanically associated with the framework. Schimper recognized that the plasma structures do not necessarily arise from the undifferentiated plasma but probably arise as do nuclei by the division of preëxisting structures of the same sort. Chodat agreed in general with Pringsheim and Tschirch as to the spongy structure of the chloroplast. Bredow found that the ground substance of the chlorophyll bodies is not composed of fibrils. Kerner held that the groundwork of the chlorophyll granules differs but little in structure and composition from the surrounding protoplasm. Wagner observed in certain cases a distinct fibrillar arrangement of the chlorophyll within the chloroplast. He was inclined to the view that the chlorophyll corpuscle consists of a ground substance in the form of a delicate alveolar structure, in which the chlorophyll is more or less diffused.

Mereschkowsky believed that the chromatophores are not organs which have been differentiated from cell plasma but foreign bodies or organisms enclosed in the colorless plasma of the cell and existing symbiotically with it. A plant cell is nothing more than an animal cell with Cyanophyceae contained in it. Plants thus have been derived from animals. Others are of the opinion that chloroplasts have been formed from mitochondria; Meyer, however, is opposed to this conclusion. Liebaldt accepted the hypothesis that the green lipoid phase and the hydroid phase exist as fine emulsoids.

This brief summary shows us that our concept of the chloroplast is not at all a definite one. There seem to be about as many concepts of the chloroplast as there are workers. Just what general idea is most prevalent regarding the chloroplast would be very difficult to state. Let us now take a closer view of the oil which is present in the chloroplasts.

Sachs observed that sometimes drops of oil form in the interior of the chloroplast.

Briosi was the first to recognize oil droplets in the chloroplast as perfectly normal inclusions and did not consider the oil as a result of a pathological condition. He showed that in several species of *Strelitzia* and *Musa* no starch occurs. Oil droplets instead of starch grains arise in the chloroplasts of these plants and this oil exists in finely divided particles between the "protoplasmic molecules" of the chloroplasts. In this connection it is interesting to note that Pringsheim thought that the green pigment is only mechanically associated with the framework.

Bredow found that oil droplets were present now and then in the meshes of the chloroplasts. Liebaldt considered that the chloroplasts of the higher plants consisted of two phases, a hydroid phase and a green one of lipoid character. The chloroplasts appeared to be homogeneously green or finely granular. Because of the fact that in most cases no definite

special division of the two components, chlorophyll and the ground substance, could be observed, he was led to accept the hypothesis that the lipoid and the hydroid exist as fine emulsions. Meyer concluded from his studies on *Tropaeolum majus* that the "grana" are small oil droplets always to be met with in the growing chloroplasts.

Stern on investigating the fluorescent properties of chlorophyll came to the conclusion that as contained in the uninjured cell it is in a true lipoid solution. Mangenot considered oil as the first product of the photosynthetic activity of the chlorophyll of *Vaucheria*.

Chlorophyll is variously stated to be dissolved in some oily substance which is held in the channels and meshes of the plastids or to exist in the form of a colloid. From all of the evidence that can be obtained it is evident that oil must exist in all of the chloroplasts. This means that chlorophyll and oil must exist together in all green plants. However, Zirkle says that when chloroplasts are tested for oil the results are quite inconclusive.

The nature of the boundary of the chloroplast has been a subject concerning which there has been much discussion. Many investigators have observed that when two chloroplasts come in contact with each other the two green masses remain intact and are separated by a colorless zone. Tschirch cited this fact to prove that a membrane exists surrounding the chromatophore. Chodat believed that the appearance of this colorless zone is due to the fact that the outer layer of the ground substance is colorless, and held that no membrane was present. Meyer held that each chromatophore is surrounded by a non-granular layer of cytoplasm. Most of the earlier workers believed that chromatophores were vesicles and Nägeli at one time stated that each chromatophore was surrounded by a cellulose membrane. Later workers, as von Mohl, Sachs and Meyer, do not admit the presence of a membrane about the chloroplast.

Some more recent investigators have denied and some have affirmed that a membrane exists. Here by membrane is meant a thin firm layer which is probably conceived to be semipermeable. Zirkle in a recent investigation recognized no such structure.

Today we recognize such things as liquid membranes, and Zirkle sees no reason why we cannot consider this inner film of the cytoplasmic sheath as such a membrane. The observed swelling of chromatophores in pure water or in aqueous solution of low osmotic value does not seem to be due to any osmotic property of this membrane, for that portion of the chloroplast which swells seems to be located within the ground substance. Modern methods of investigation also show us that a colorless zone such as was noted by Tschirch and Chodat can be readily demonstrated in the living cells of *Elodea*. The thickness of this zone varies from 1 to 0.25 micron and seems to be correlated with the state of the cytoplasm. When cyclosis is very sluggish the zone is thick; when the cell contents are rapidly circulating the zone is thin. No distinct zone could be observed at all when the chloroplasts were rapidly moving. Evidence shows that the chloroplast covering remains with it when it circulates in the cell; yet this layer is not constantly associated with the chloroplast, for its thickness is continually changing.

Workers have generally agreed that the ground substance of the chromatophore is a protein. It is true that Mulder considered it a wax derived from starch and

some of the earlier workers thought that it was starch. However, the staining properties of the ground substance indicate that it is a protein. In general, the reaction of chloroplasts to the histological stains shows that they contain protein. Also, the proteolytic enzymes, pepsin and bromolin, will digest the chloroplasts. The evidence shows that there is no doubt as to the real nature of the ground substance of which the chloroplast is composed. There also appears to be no argument as to whether there is or is not a true ground substance. However, there is an argument concerning the physical state of the ground substance.

Zirkle says that the physical state of the ground substance is a gel rather than a sol, which can be demonstrated by tearing apart the chromatophores. Besides it is hard to conceive of a sol maintaining a definite structure such as the ground substance possesses in the living cell. Since there has been so little investigation on this subject it cannot be said that the matter is definitely settled yet. Something has already been said regarding the location of the pigments in the chloroplasts but a summary of our ideas on this subject will be beneficial at this time.

The opinion is generally, though not unanimously, held that the chloroplast pigments are more or less restricted to the peripheral region. Investigators who have noticed the granular appearance of the chromatophores are almost equally divided as to whether the important pigments are located in the granules themselves or in the ground substance in which the granules are imbedded. Lloyd observed that it is the non-granular part of the stroma which emits fluorescent light. Sachs believed that both granules and ground substance are colored, while Chodat thought that the lacunae within pigment layer. Zirkle found by examining the chloroplasts in light of various wave lengths, corresponding to the absorption band of each of the different pigments, that the pigments are intimately mixed and evenly distributed throughout the ground substance. The only parts of the chloroplasts not colored were the pores and the starch inclusions.

The state of chlorophyll in the chloroplast has been investigated by many workers. Reinke investigated the properties of the pigment chlorophyll both within the living plastid and in solution. He found a slight fluorescence in the living, green plastid and assumed that there must be some sort of combination between pigment and plastid and that the pigment existed not as a solution but as finely divided particles.

Herlitzka in investigating the absorption spectra of chlorophyll concluded that it is held in a solution of different form from that of its usual solutions with organic solvents; this form being that of a colloidal solution. Iwanowski came to the conclusion that chlorophyll must exist in a colloidal form in the living chloroplast, for it is in the latter state that it is most indestructible.

Stern seems to possess a slightly different view from most investigators, for he observed that chloroplasts fluoresce somewhat, and this led him to the view that chlorophyll is present in the cell in a true lipoid solution.

Lloyd brings forth evidence to show that chlorophyll does not exist in solution in the chloroplast but that it is present in some other form. Later in the same year he found that chloroplasts of leaves and of green algae show a deep red fluorescence to a marked degree. He finds that the part of the chloroplast which emits fluorescent light is the non-granular stroma.

in the leaves by capillary attraction, while Tswett thought that the pigment is bound to the framework of the chloroplasts by molecular absorption forces. Willstätter once explained the peculiar behavior of chlorophyll in the leaves toward solvents by the assumption that the chlorophyll probably occurs in the leaf substance in the form of absorption compounds with colloids. Palladin thought that the chlorophyll is held bound in the leaves in a chemically combined condition with phosphatides. Spectroscopic evidence shows that the absorption bands in the spectrum of living leaves are displaced with respect to the spectrum of a chlorophyll extract toward the more weakly refracted end. Iwanowski finds that the spectra of leaves and of colloidal chlorophyll solutions are similar to each other but not identical. He assumes that the chlorophyll is not dissolved in the leaf as a colloid but is present as a fine suspension. Willstätter (1913) believes that the chlorophyll is present in the leaves in a colloidal state of distribution or in a very similar condition. Zirkle is of the opinion that whatever the union between the chlorophyll and the ground substance may be, it is not a very strong one, as it can easily be destroyed by many solvents. The union does not seem to affect any of the properties of chlorophyll, while the presence of chlorophyll within the plastid does alter certain properties of the latter. In the first part of this paper the writer has attempted to show that only two carotinoids are present in the chloroplasts.

A brief review will now be given of the number of the green pigments.

Lubimenko inferred from his absorption experiments that there was only one green substance in leaves and that this is broken down by ordinary methods of extraction into chlorophyll a and b and the yellow pigments. Sorby as well as Tswett found evidence of three chlorophylls in the brown algae but later Willstätter and Page found no trace of the third component. They found that the chlorophyll of brown algae consisted mostly of chlorophyll a and only traces of chlorophyll b. Wlodek by means of a spectrometer has demonstrated that there are only two chlorophylls. It is now known that land plants contain about three parts of a to one of b. The history of the two pigments and the difficulties attending their separation need not be related here. It is sufficient to say that it is commonly recognized that there are two and only two green pigments present in all green plants.

THE CHEMICAL INVESTIGATION OF CHLOROPHYLL

The chemical investigation of chlorophyll probably began with Berzelius, who first undertook to isolate the green pigment from leaves. He used concentrated acids and alkalies, believing that the pigment was not injured by these chemicals.

The work of Berzelius undoubtedly had much influence upon later workers as Mulder, Morot, Verdeil and others. To Verdeil we owe our first knowledge regarding the relationship of the coloring matter of blood and of leaves. Chlorophyll and blood both were considered to contain iron, and this view was maintained for a long time. Fremy investigated the relationship of the green and yellow pigments. Hoppe-Seyler agreed with Verdeil's ideas regarding blood and chlorophyll and developed further Fremy's lecithin hypothesis of chlorophyll. Hoppe-Seyler later attempted to isolate chlorophyll avoiding energetic reagents. A substance called chlorophyllan was obtained by alcoholic extraction, but this was not chlorophyll at all. Stoklasa even as late as 1907 found potassium and phosphorus present in chlorophyll. It was

Hoppe-Seyler who first discovered phylloporphyrin, which definitely established the blood-chlorophyll relation.

Nencki and Zaleski obtained hemopyrrole from hemin by reduction, while in the same year Nencki and Marchlewski obtained it by reduction from phyllocyanin. From this it at once became evident that the molecules of hematoporphyrin and phylloporphyrin consist of the same or closely related constituent parts. Willstätter and Asahina have shown that the composition of hemopyrrole is not as simple as was assumed and that it consists of a mixture of pyrrole homologs containing a tetra substituted pyrrole and in which the trisubstituted pyrroles predominate. After Hoppe-Seyler chemical workers did not attempt to isolate and analyze chlorophyll. Much work, however, was done on the cleavage products but nothing of great value was discovered. Even up to the time of the work of Willstätter none of the chemical characteristics of chlorophyll were known.

Since during all of the previous investigations no chemical characteristics were established for chlorophyll, it was not possible to compare the chlorophyll of different plants. Because of this situation opinions differed widely regarding the identity or dissimilarity of the pigments in different plants. Gautier believed that the chlorophyll of monocotyledonous plants was different from that of dicotyledonous ones. Etard in 1906 published a book in which he described a long series of different chlorophylls from one plant and an unlimited number of chlorophylls from different plants. A different chemical formula was given for each of these. Stokes hinted at the existence of two chlorophylls, but his observations went unheeded among the prominent scientists. Borodin discovered crystals of chlorophyll, but analysts failed to follow up his investigations. Monteverde isolated the crystals and determined their properties spectroscopically. Willstätter and Benz (1907) by working on a large scale obtained crystallized chlorophyll, at a time when its analysis had already been accomplished by indirect methods. Chlorophyll as a pure chemical substance has been known for only a few years.

Hoppe-Seyler found that phosphorus was present in chlorophyll and believed that it belonged to the lecithins. His hypothesis was ardently upheld by Stoklasa even up to the year 1913, when he was firmly convinced that potassium and phosphorus are present in the chlorophyll molecule. We now know that the chlorophyll molecule consists of carbon, oxygen, hydrogen, nitrogen and magnesium.

Till Willstätter isolated chlorophyll just what chemical elements were present in the molecule was not known with certainty. Indeed, little more was known than that its decomposition products belonged to the pyrrole derivatives. Willstätter and his coworkers first deduced the characteristics of chlorophyll from a consideration of the derivatives which were formed by reactions with acids and alkalies. At first the task appeared hopeless because of the alterability and chemical indifference of chlorophyll and on account of the extreme solubility of the pigment when diluted with so many colorless and yellow admixed substances. Phytol was found to make up a third of the chlorophyll molecule. The "crystallized chlorophyll" was found to be free of phytol, while the amorphous pigment contained it as a constituent of the molecule. The results which they obtained showed that chlorophyll is identical in all plants and consists of two components, a and b. The two components were found to agree in their phytol and in their

magnesium content and were also very similar in the composition of their basic nuclei.

Willstätter and Stoll are of the opinion that further investigation is necessary to fix and strengthen our conception of the chlorophyll molecule. It is well to note here that by the most drastic treatment with acids and alkalies nitrogen always remains in the decomposition products. It is interesting too to note that there are four nitrogens and that each is bound in the form of pyrrole. Etioporphyrin, the parent substance of blood and chlorophyll, is composed of four pyrrole nuclei. Reduction of the porphyrins yields hemopyrrole, which is also known as the reduction product of blood dyestuff.

Nencki and Marchlewski were the first to obtain it from a chlorophyll derivative. Willstätter and Asahina have shown that hemopyrrole has a surprisingly complicated composition, being a mixture of at least three components. Phyllopyrrole, a tetra-substituted pyrrole, has been isolated from the mixture. Phyllopyrrole, isohemopyrrole and cryptopyrrole are now known as components of chlorophyll because of the work of Fischer and Bartholomaeus and Piloty and Knorr. Other pyrrole constituents also are present. Phyllopyrrole is distinguished from the pyrrole bases with eight carbon atoms principally by the absence of the pine splinter reaction and of the color reaction with dimethylamino-benzaldehyde. Also, it is not precipitated in an acid solution by a diazonium salt. It was considered a pyrrole, for it took up four atoms of hydrogen and produced a saturated hydroderivative. The pine shaving reaction is, analogously to the dimethylamino-benzaldehyde reaction, to be understood as a condensation of the aldehydes of the wood with the pyrrole nucleus. Feist has shown that pyrroles substituted at all four carbon atoms cannot condense with aldehydes, and Fischer had noticed that pyrroles similarly substituted do not give the Ehrlich reaction. Also phyllopyrrole is not precipitated by an aqueous mercuric chloride solution, which is contrary to statements in the literature.

When chlorophyll, as well as when hemin, is reduced a mixture of different pyrroles is always formed. A review of the literature will easily convince one that our knowledge regarding pyrroles is very elementary and that there is much need for further work on these decomposition products of chlorophyll and of the blood pigment.

Those who have never worked with chlorophyll do not realize some of the difficulties involved in its preparation. Chlorophyll as a pure chemical substance was not isolated in an undamaged condition and free from accompanying materials until all of its physical and chemical properties were known. Colorless accompanying materials, fats, waxes and salts of fatty acids accompany the pigment and distribute themselves among the different solvents in much the same ratio as chlorophyll does. Because the pigment was so easily soluble in all solvents its purification was very difficult. Chlorophyll of a certain degree of purity is no longer soluble in petroleum ether which is free of alcohol. After this fact was known the preparation of chlorophyll was soon accomplished. At first the yields were very small but now 8 to 10 grams of pure chlorophyll may be obtained from each kilogram of dry nettle leaves. At the present time, pure chlorophyll, crude chlorophyll, pheophytin and the copper salts of chlorophyll may be easily prepared and some are now being prepared by the ton. Let us now turn our attention to some of the factors affecting chlorophyll. The effect of light will be considered first.

FACTORS AFFECTING CHLOROPHYLL

Chlorophyll does not usually develop in leaves grown in the dark, as illustrated by the colorless sprouts of potatoes or onions grown in a dark cellar, and it gradually disappears from green parts denied light as in the blanching of celery when banked with earth. It is soon destroyed by bright light, the plant remaining green only because of its continual renewal brought about by the agency of light in the active plant. In autumn when the plant no longer produces chlorophyll it disappears, being bleached to colorless products.

On the other hand we find that in green plants chlorophyll may occur not only where light gains access to the living cells but also in places where it seemingly cannot penetrate, at any rate in any quantity, for instance in the cortex internal to the periderm, in the medullary rays and even in the pith. Chlorophyll may occur in the cotyledons of seeds before they are set free from the ovary or from the cone; species of *Cucurbita* and *Pinus* are familiar examples. In these cases the influence of the light which may penetrate the cells is not known. However, it is known that if sugars and other foods are present in sufficient amount, conifer seedlings, various ferns and liverworts, and many algae become green, even in total darkness, and a number of angiosperm seedlings become green in the dark if the fruits in which the seeds develop are produced in the light.

On the other hand algae may lose their green color when grown in rich nutrient media in the light.

Because chlorophyll is present it does not necessarily follow that photosynthesis takes place, even though the requisite conditions obtain. In the case of green parasites it appears as if the chlorophyll is not functional, or at any rate its photosynthetic power is so small as to be masked by the respiratory activity. Nothing definite is known regarding the substances which immediately precede chlorophyll formation.

Regarding the stability of chlorophyll in chloroplasts, Iwanowski has found that it is destroyed by light in solutions of various concentration, and he found that the more concentrated the solution the less susceptible it is to destruction by light. Chlorophyll in a true solution, regardless of concentration, is more easily destroyed than in the living leaf. The yellow pigments he believed protected the chlorophyll from decomposition by light.

Wurmser claimed that the resistance shown by the chlorophyll in the living cell to the destructive action of light is due to its being protected by colloids.

Very weak light is favorable for chlorophyll formation, while light of medium intensity is most favorable. Famintsyn exposed a part of an etiolated plant to direct sunlight, while the intensity of the light falling upon the remaining portion was reduced by interposing sheets of paper; greening always occurred first in the reduced light. According to Wiesner this phenomenon is to be explained by supposing that decomposition and formation of chlorophyll occur simultaneously. In light of low or medium intensity the decomposition process is nearly absent, while in strong light active formation is accompanied by rapid breaking down of the chlorophyll, which results in less pronounced greening than occurs in diffuse light. Wiesner has found that various parts of the spectrum have different effects upon the formation of chlorophyll. The effect of light and of different portions of the spectrum upon chlorophyll is a subject of great importance. Studies should be made of its effect upon chlorophyll in

solution as well as of its effect upon chlorophyll in the plant.

The work of Oddo and Pollacci must be considered in a review of this kind. They found that corn, *Datura*, *Solanum*, *Euphorbia* and asters grown in solutions containing magnesium pyrrole-di-carboxylate were normal, while plants grown in a solution which did not contain this pyrrole compound were chlorotic. When pyrrole was present even in the absence of iron, greening was observed. Referring to Mamelis' work they believe that pyrrole and magnesium are the factors which determine the green coloration of plants. In this connection it is interesting to note that Kraybill in working on tomatoes found that dried blood caused the plants to be deeper green and more vigorous. One cannot help wondering whether the blood has been ammonified or whether the nitrogen has been absorbed while still in the pyrrole form. We are forced to question whether the following statement so often found in the literature is correct: it is only after decomposition and conversion into ammonia and nitrates that the numerous important organic nitrogen fertilizers are to any practical extent valuable for plants. Ciamician and Galizzi report that certain pyrrole compounds are not toxic to plants, while Emerson reports that pyrrole compounds have been used in nutrient solutions with varying success. Deuber's work seems to show that the pyrrole compound used by him is toxic to plants. Just what the real situation is in regard to pyrrole compounds would be difficult to say from the small amount of work which has been done upon the relation of pyrrole to plant growth. In Deuber's work it is interesting, however, to note the luxuriant development of bacteria in the cultures which contained the pyrrole compound. Schreiner and Skinner studied the effect of nitrogen compounds upon the growth of plants and paved the way for work which at the present time offers much promise in the realms of plant physiology.

We are also led to wonder about the factors which influence photosynthesis. Just what are the limiting factors anyway? Briggs and Irving conclude that the power of photosynthesis lies behind the development of chlorophyll. The photosynthetic power of a leaf increases with age even though there is no concurrent increase in the chlorophyll content. Others believe that there is an internal factor, independent of chlorophyll and associated with protoplasm, which controls the rate of carbon assimilation. Since the assimilation numbers arrived at by Willstätter and Stoll are not constant this is very strong evidence that chlorophyll is not the all important factor in photosynthesis. They believed that an enzyme limits carbon assimilation. Even to this day nobody has succeeded in bringing about carbon assimilation by means of chlorophyll which has been isolated from the leaf.

This brings us to the factors which influence the formation of chlorophyll. Light, temperature, iron, mineral salts, oxygen, carbohydrates and others seem to be the factors which are stressed mostly in our modern texts. It is very remarkable that the element nitrogen does not seem to be given a place as a possible factor in chlorophyll formation. In one of our most modern texts some such statement as this is found: iron salts and nitrates are regarded as favorable for chlorophyll development. Others make no mention of any possible relation between nitrogen and the green pigment. Nitrogen has been considered more in its relation to proteins. However, a few have seen a possible relation of nitrogen to the color of green plants.

It was Ville who first showed that nitro-

gen played a rôle more important than that of any of the other elements tested. If the dose of nitrogen was increased or diminished the color of the plants increased or diminished also. Urban found that the darker beet leaves contained the most nitrogen and the lighter the least. Wlodek observed that the width of the absorption bands correlated with the nitrogen content of the leaves. Sir John Russell in discussing the effect of fertilizer upon plant growth said that nitrogen produced larger leaves and stems. A greater formation of green coloring was induced. The writer has shown in his work on *Coleus* that nitrogen appears to be one of the limiting factors in chlorophyll formation. It was also shown that after adding nitrate to a plant only a few days were required before a greening showed up in the leaves. Eckerson observed that simultaneously with the appearance of amino acids the chloroplasts of the younger leaves became greener, in from three to five days after the addition of nitrates. The chloroplasts of the deep green leaves of *Tropaeolum*, as noted by Meyer, were larger than those of the pale green leaves. Size of the chloroplasts and color of the leaves were definitely correlated. He looked upon the chloroplast as the birthplace of the proteins, hence it is easy to see why the color of the leaves and the protein content are so intimately related. He observed also that as the leaves yellowed there was little change in the size of the nucleus, the nucleolus, or in the protein content of the cytoplasm. He inferred that the formation of chlorophyll in the chloroplasts follows the development of protein in the leaves.

Allison in considering nitrogen as a plant food says that of the ten elements commonly considered as essential plant foods, nitrogen stands out in many ways as the most important. Not only is it deficient in many soils, expensive to supply and difficult to retain, but it plays an exceedingly important part in plant metabolism, including both the constructive changes and also the respiratory reactions resulting in the destruction of carbohydrates and proteins. These reactions apparently take place within the plant cells, the synthetic reactions being confined largely to the leaves and active growing portions of the plants, while the respiratory changes which result in carbon dioxide production may occur throughout the plant tissues. Without doubt the nitrogen compounds present in the protoplasm of the cells as protein, amino acids or other compounds are the active constituents which enable the tissue building to proceed. Without nitrogen there could be no life upon the earth.

The writer has observed a definite correlation in cotton leaves between the size of the chloroplasts, the color of the leaves and the amount of nitrogen which has been added to the soil in which the plants grew. He has also found that in the case of potatoes a high chlorophyll content of the leaves is correlated with high nitrogen fertilization. In the case of cotton, leaves from plots high in nitrogen contained more of the chloroplast pigments than did those from other plots. Without forgetting the relation of nitrogen to the development of chlorophyll, the latter will be considered as a limiting factor in the growth of plants.

Briggs in working on vegetable assimilation and respiration found some very good lines of evidence regarding the chlorophyll factor in plant growth. It appears, he says, that the inevitable conclusion to be drawn is that increase in assimilation with progress of time cannot be due to increase in chlorophyll content during that time, increase in leaf area, fall in respiration or a combination of these

factors, but must be attributed to increase in some internal factor other than chlorophyll. Further indications seem to show that this factor is dependent upon chlorophyll and some other factor working in correlation with chlorophyll.

Irving also has concluded that the development of photosynthetic activity in the young leaves of seedlings lagged behind greening, which means that it is dependent upon some factor other than chlorophyll.

Willstätter and Stoll have come to the opposite conclusions and think that chlorophyll is a limiting factor.

Briggs believes that there are three lines of evidence indicating that chlorophyll is not the limiting factor in the young stage of leaf development. He says that in the case of Irving's experiments the chlorophyll continues to increase to a certain point without any sign of assimilation. In the case of Willstätter's young leaves, as in the case of those of Irving, when they once reached the stage of beginning to assimilate, the assimilation increased out of proportion to the increase in chlorophyll and lastly Briggs has found that assimilation increases while there is no increase in chlorophyll.

ATTEMPTS MADE TO RELATE VITAMINES TO THE CAROTINOIDS AND TO PHYTOL

For years attempts have been made to find out a possible relation of the vitamines to the chloroplasts of leaves and especially to the carotinoids. A review will now be made of this possible relation. Before proceeding with the discussion it may be stated that no attempt has yet been made by anyone to associate vitamines with the water soluble pigments, flavones and anthocyanins. Vitamines, especially A, have always been associated with the lipochromes, which association will now be taken up.

Since vitamine A is closely associated with the lipochromes in animal fats many workers were led to speculate on the possible identity of vitamine A with one of the lipochromes. Drummond showed that there was no foundation for this belief by preparing pure carotin from carrots and demonstrating its complete lack of growth promoting power. Others have shown that many animal fats which were rich in carotin were relatively poor in vitamine A and that in other fats the reverse relation held. Steenbock, Sell and Bluell pointed out that the concentrations of lipochromes and vitamine A in butter were not closely parallel though they were in general agreement and suggested that this might be due to their having the same source in the green food of the cow. In six different varieties of dried peas a greater vitamine content ran parallel with a greater lipochrome content. White sweet potatoes and white carrots, in marked contrast to the yellow varieties, contained little vitamine A.

Coward says that lipochromes are present in many seedlings before the appearance of vitamines. A comparison of the lipochrome in shoots which will not promote growth with that in shoots which will promote it proves that the activity of the tissue is not measured by its lipochrome content. Other instances of association of vitamine A with lipochrome in plant tissues are afforded by tomato pulp, cucumber skin, yellow sepals and petals, orange juice and red and yellow capsicum fruit. The absence of vitamin A is associated with absence of lipochromes in mangolds, swedes, cauliflower, corollas of Shasta daisy and of purple aster. Lipochrome (generally carotin) is always associated with vitamine A in plant

tissues, and where carotin is found, particularly carotin exposed to sunlight, there the vitamine may be expected to be present also.

Fat soluble vitamine has been shown to be intimately associated with yellow pigment. Maize, carrots and sweet potatoes which are highly impregnated with the yellow pigment were found to supplement successfully rations known to be deficient in fat soluble vitamine. Roots not pigmented were found to be impotent. Butter rich in pigment and also oils containing the yellow pigment show a considerable fat-soluble vitamine content. In the case of the leafy parts of plants the growth promoting property is associated with the yellow pigments, though here the yellow pigments are masked by the chlorophyll.

Regarding the relation of vitamines to lipochromes, Palmer says that he dismissed the possibility of any such relation as the result of experiments carried out in the winter of 1916–17, in which normal chickens were raised to maturity on carotinoid-free rations. Drummond in 1919 reported the failure of pure crystalline carotin to improve the condition of albino rats suffering from vitamine A deficiency, while at the same time Steenbock, Boutwell and Kent were suggesting that the two were at least associated in some way. Steenbock and his associates have published a series of papers showing that a rather close correlation exists between carotinoid pigmentation and vitamin A. Steenbock and Boutwell's results show that highly colored extracts do not exhibit the vitamine activity which would be expected if vitamine A were a carotinoid. Steenbock has been forced to abandon his position that the two substances may be identical and to admit that their "coincident occurrence in nature might be due to physiological determination, pure and simple."

The lack of correlation between pigmentation and vitamine content of animal fats was first pointed out by Drummond and Coward in 1920. Further proof that vitamine A is not necessarily associated with carotinoids was furnished by Palmer and Kennedy, who grew normal rats on carotinoid-free diet.

An association of carotinoids with other vitamines than vitamine A has also been suggested, but Palmer says that it hardly seems possible that anyone with a thorough knowledge of the distribution and properties of vitamine B could give this suggestion any serious thought.

In Palmer's book on the carotinoids he states that the yellow pigments may be considered in three possible relations, which have a bearing on the vitamine situation.

In the first place, Rosenheim and Drummond have expressed the view that the deflection of xanthophyll to the ovaries during egg laying indicates that the pigment is required for a definite and important function in the egg and that this fact supports the theory that the carotinoids are related to the vitamines.

However, Palmer says that it is just as reasonable to suppose that the egg yolk is an easier path of excretion for a fat soluble pigment than the skin, just as the kidneys are ordinarily the chief path of excretion of water soluble waste products.

Lastly, it is known from experiments that Nile blue is transported to the pigment granules in the epidermis of the chicken skin in association with fatty acids. When salmon migrate to the spawning bed they eat nothing. When the fish come from the sea their flesh is a strong pink color while the small ovaries are yellow brown. As the reproductive

organs develop the flesh becomes paler and the rapidly growing ovaries acquire a fine orange red color. Palmer suggests that the explanation of this phenomenon lies in the mobilization of the fat stores of the body in the reproductive organs and the shed ova rather than in the mobilization of the pigment itself.

Thus, there are three views regarding the carotinoid-lipoid relation, the most logical of which is that the pigment is mobilized along with the food which is stored in the egg, and this idea would support the theory that carotinoids and vitamines are not related in any way. The fact that the yellow pigments are deflected from the normal path of excretion and are found in the milk and in egg yolks does not necessarily mean that they are useful.

Javillier, Baude and Lajeunesse have looked in another direction for a solution of the vitamine question than have most workers. They experimented to ascertain if factor A had any relation to phytol, a derivative of chlorophyll. From their experiments they concluded that phytol is not vitamine A.

In this part of the paper the writer has attempted to assemble some of the evidence showing that the vitamines are not carotin or xanthophyll and that they are not phytol, a chlorophyll derivative. As far as the plant pigments are concerned there seems to be only one other possibility. That possibility will now be considered by reviewing what various authors have to say on the subject.

PROBABLE RELATION OF CHLOROPHYLL TO THE VITAMINES. CHEMICAL ELEMENTS PRESENT IN VITAMINES

Before we take up that possible relation it would not be out of place to mention here that some have sought to associate the rôle of vitamines with the general body metabolism. Fünk, Bradden and Cooper sought to establish a relation between vitamine B and carbohydrate metabolism. Drummond investigated the effect of vitamine B on nitrogen metabolism and the effect of vitamine A on fat metabolism.

At this point a definition of vitamines might assist us somewhat in our search for them. Randoin and Simonnet say that vitamines are substances not yet chemically or physically identified, which the animal organism is incapable of synthesizing, which are obtained in certain fractions of the undetermined portions of the food and which in exceedingly small amounts are indispensable to the vital phenomena during the course of development of the animal or in its adult condition and whose absence is responsible for characteristic disturbances of nutrition.

No vitamine has yet been isolated. If it is not the lability of the compound in question, it is its extreme chemical indifference to such reagents as are ordinarily used to modify solubilities that prevents its separation from its environment. The present state of our knowledge is such that any indication as to the probable nature of a vitamine is worthy of investigation. The chemical and physical properties of any one of the vitamines are not very well known. Autoclaving at 15 pounds pressure for three hours did not destroy any of vitamine A as found in yellow corn, nor did this treatment cause any noticeable destruction of the vitamine in chard, carrots, sweet potatoes and squash. Experiments have demonstrated that vitamine A as found in the plant kingdom in grains, leaf and stem tissue, in fleshy roots and in vegetables is comparatively stable at a high temperature.

Vitamine A is destroyed by long exposure to light and air. When melted

butter has been poured into shallow dishes and then exposed to direct light and bleached, vitamine A is destroyed.

Oat straw is low in vitamine A but oat hay dried out of direct sunlight appears to retain the properties of fresh green oats. It has been noted also that alfalfa hay cured under caps and that cured in the windrow with a comparatively distinct difference in respect to time of exposure to light and air have great differences in their vitamine content.

To describe all of the supposed physical and chemical properties of the vitamines would be a procedure too lengthy for the purpose of this paper. It is of interest, however, to note what chemical elements are thought to play a part in the vitamine molecule. In the case of vitamine B analysis shows that it possibly contains carbon, hydrogen, oxygen and nitrogen. Many workers agree that the molecule contains nitrogen. Some of the investigators believe that vitamine A contains carbon, hydrogen and nitrogen. At least it has become quite firmly established that nitrogen is present in the vitamine molecule.

In regard to one of the vitamines, Sherman and Smith say that partly from its solubilities and its greater stability in acid than in alkaline solution and partly from the results of attempts at isolation, it appeared probable at a relatively early stage in the study of this vitamine that it was a nitrogenous base very probably related to the purines or pyrimidines. It is perhaps a hopeful sign that later evidence, both from attempts at its isolation and from studies of its physiological behavior, does not in the main contradict the earlier indications.

RELATION OF VITAMINES TO PLANT TISSUES

In reviewing the relation of vitamines to plant tissues, a logical starting point would be the seeds of plants. Seeds in general are poor sources of vitamine A. Fürst, Chick and Hume have shown that vitamine C is not present in dry seeds but is produced during germination. Both dry and germinated peas are deficient in vitamine A.

Just what part the vitamines play in the germination of seeds is not definitely known. They may be important in the first stages of metabolism; perhaps they are responsible for the onset of cell division. They may exert some influence upon the nucleus and protoplasm partition.

In the case of animals, Sweboda by using the yeast multiplication method finds that the organs of internal secretion which are of developmental importance are relatively rich in vitamine B. The pituitary and pineal glands are highest in vitamine content, and most of the other organs of internal secretion—suprarenal, testis, ovaries, and thyroid—contain about the same amount of vitamine per gram of dried tissue. He emphasizes the prominence of vitamine B in those organs which are important in connection with sex development.

Coward and Drummond are of the opinion that the amount of vitamine A present in etiolated shoots of peas is not appreciably greater than that in the seed from which it grew. Green shoots possess a decidedly higher value as sources of vitamine A than either the seeds from which they sprang or the corresponding etiolated shoots.

According to Wilson it is generally believed that the synthesis of vitamine A takes place only in plants. The green parts of plants appear to be among the richest sources of the vitamine, whereas seeds in general contain only traces of it. It seems apparent therefore that the plant must synthesize vitamine A found so abundantly in its leaves. Since most

plant syntheses are dependent upon solar energy it appeared desirable to find out whether or not the production of vitamine A is dependent upon photosynthesis. His experiments have led him to conclude that photosynthesis is not necessary for the production of vitamine A in plants, for wheat sprouts grown in either the dark or the light seemed to be adequate sources of vitamine A. The green sprouts apparently were more active than the etiolated ones.

On the other hand, Coward has found that light is necessary for the formation of vitamine A in plant tissues. An investigation of some of her results on the effect of carbon dioxide, oxygen and chloroform shows that much more work is necessary before any conclusion can be drawn regarding these factors.

It is reasonable to conclude, say Coward and Drummond, that the formation of the large amounts of vitamine A found in the green leaves of most plants demands the influence of light.

On the other hand the carrot and the sweet potato are examples showing that vitamines may be present in tissues which are not exposed to sunlight. It has been questioned whether the vitamine has been formed in the root of the carrot or whether it has been transported there from the leaves, where it is definitely known to occur. Coward has shown that the vitamines and carotin can be transferred upward from the carrot to its leaves, and there is no reason to believe that the reverse process can not take place.

Coward and Drummond believe that the fat soluble vitamine occurs in the green actively assimilating parts of plant tissue and that it is generally absent from the localities where chlorophyll is not found. Lower organisms devoid of chlorophyll do not seem to synthesize vitamine A. It is known also that the outer green leaves of cabbage contain more vitamine A than the white inner leaves.

The common green seaweeds contain as much vitamine A as do green land plants such as cabbage. It is believed that this is not present in the form of a complex with protein in green leaves. Vitamine A can be extracted from green leaves by fat solvents and can also be obtained in the unsaponifiable fraction of the fatty substances extracted from green leaves.

Coward says that its absence from etiolated leaves, or those which have never been exposed to the light, has been shown and likewise its presence in all plant tissues so far examined which contain lipochromes and which have also been exposed to the light. In the case of underground structures, the only ones found to contain more than the merest trace are the carrot and the yellow sweet potato, each of these also containing lipochromes. Comparisons between different green vegetables or salads have sometimes been made regarding the vitamine content, but apparently very little consideration has been paid to the possible differences of vitamine content of leaves of the same plant grown or preserved under different conditions. Attention has been called to the difference in the vitamine content of two different samples of hay, but the difference was ascribed to the method of curing rather than to a difference in the hay on cutting. Some have noted a very marked difference in the vitamine A content of butters made from the milk of cows fed at the beginning of the experiment on a sample of hay which had been cut when growing vigorously and later on hay which had been cut when it was beginning to wither. The difference in the butters has been shown to have been due to the difference in the vitamine content of the two samples of hay by

feeding the hay itself to rats. Observations have shown that shoots of *Tradescantia* kept in water culture solution in the dark for some eight weeks had lost only very little of their vitamine activity. Sunflower seedlings exposed to the light and then kept in the dark for eight days had apparently lost none of their activity. Because of the above results Coward decided to investigate the persistence of vitamine A in plant tissues more fully. Her observations show that vitamine A is not used up in any process carried on by living plant tissue in the dark. The vitamine appears to increase when a leaf loses its green color and becomes yellow. Growth obtained with fresh yellow leaves was at least as good as that obtained with the green and appeared to be even better. Withered leaves which had passed through the clear yellow stage, fallen from the tree and died, gave no growth. It appears that vitamine A is not used up in the yellowing autumn leaf until it actually dies. This vitamine was shown also not to diffuse appreciably into water from the cut ends of shoots.

The presence of vitamines B and C in certain parts of plants has already been shown; no account, therefore, will be given of them here.

According to Mockeridge, it appears probable that all the animal vitamines are direct products of plant synthesis. It has been ascertained by numerous workers that animals obtain their necessary vitamines from their plant food. It is now established that plants in their turn require growth-promoting substances which in the case of some of the lower plants are apparently manufactured by themselves, but which in the case of green plants must be supplied from without. Since these necessary accessory substances are essentially organic in nature, their only possible source in the case of ordinary green plants is to be found in the organic matter of the soil in which they are growing.

Drummond, Coward, and Watson confirm the statement of Mockeridge relative to the relation of vitamines in plants and animals. They say that milk secreted by the lactating female will tend to be deficient in vitamines unless her diet contains adequate amounts of these factors. Evidence in support of this view is growing stronger as data accumulate. The value of butter as a source of vitamine A appears to be more dependent upon the diet of the animals than on the length of time that the butter has been in storage. Butter stored at a low temperature does not suffer any appreciable loss of vitamine A.

According to Funk, it may truly be said that no single division of physiological chemistry has lately been productive of more publications than that of the vitamines. The reason is, that new facts and observations are obtained with an ease that is truly astonishing. Because of this, many investigators have failed to penetrate more deeply into this subject. They have satisfied themselves, as a rule, with results obtained by indirect conclusions. This condition of marking time and useless quibbling provides an excellent opportunity for the representatives of destructive criticism, which, here more than in any other field of research, is effective in hindering the solution of the problem. In spite of these difficulties the knowledge of the nature of the vitamines progresses gradually, and we may hope that their chemical isolation is not far distant.

Until lately the idea was prevalent that for the complete nutrition of an animal organism only proteins, fats, carbohydrates, salts and water were necessary. However, in the older literature there is no lack of statements which of themselves

should have given rise to an eager search for additional dietary components essential to life.

It has been shown by many investigators that certain amino acids such as tyrosine, cysteine, tryptophane, histidine, arginine and lysine are more or less indispensable to the animal organism.

Hopkins made the prophetic statement that no animal can live upon a mixture of pure protein, fat and carbohydrate even when the necessary inorganic material is supplied. The animal body is adjusted to live upon the tissue of plants or animals and these contain countless substances other than protein, fat and carbohydrate.

The firmly established importance of the vitamines for the existence of certain animals and plants, organisms far removed from each other genetically, makes it apparent that these substances are of universal importance to life.

CONCLUSION

Thus far in this paper it has been only my intention to summarize what is already known regarding the subjects which have been discussed. In that which is to follow nothing new will be presented, but what has already been cited will be placed in a new order with the hope that some new relations may be discovered. This article is written with the hope of stimulating interest in the chloroplast pigments and not with the intention of proving the truth or falsity of any of the ideas herein presented. It is my desire to have the reader of this paper sit down and honestly ask himself if there is a possible relation such as will be suggested here. It is up to each one of us to decide for himself whether there is any relation or none. Conscientious thinking on the part of the reader is all that I ask. What I write is the result of ten years work and study of the chlorophyll question and is offered only as a report of progress made in the solution of the problem. Absolute proof of the real nature of chlorophyll will most likely be many years in the future. But at least for the present no harm should be done in pointing out a possible relation to other substances which have long been studied but whose real nature has never been determined.

In thinking over this problem we should keep ever in mind that Willstätter worked for many years with the green pigment of leaves before he finally isolated it. He had many workers, an abundance of funds and laboratory facilities which most of us never dream of, and even then only after many discouragements did he finally separate the pure substance, chlorophyll. A simple discovery regarding the chemical nature of chlorophyll made possible the solution of this problem. In addition to the material equipment which he had, he possessed something far more worth while than all of these, for within himself there was a determination and the desire to know the truth for the truth's sake and for no other reason. I have been told that when he found that chlorophyll contained magnesium instead of phosphorus, he was cautioned by some of his colleagues that he should go slow in publishing his findings. Instead, he soon boldly announced his results to the scientific world and for more than fourteen years his work has stood unchallenged. In fact, the story of his work on chlorophyll is as fascinating a story as may be found in the scientific world. There seemed to be one test which he applied to all of his work, and that test was that the result should satisfy himself; for he realized that if he was not honest with himself he could not expect the scientific world to accept the results of his investigations.

In regard to the history of the preparation of pure chlorophyll a point will

be well worth mentioning here. The physical and chemical properties of chlorophyll were learned gradually during the course of many experiments by a study of its chemical reactions and of its acid and alkaline decomposition products. In fact, practically all of its physical and chemical properties were known before the pure pigment was obtained and so little new was learned from studying the properties of the green pigment when isolated.

Some of the difficulties of the preparation of pure chlorophyll should be pointed out. In looking over the papers which have been published by Willstätter and his coworkers one should keep in mind the fact that he was working with a green pigment whose color was easily altered, yet when altered a pronounced color always resulted. The fact that he was working with a colored pigment in which any chemical or physical change could be easily detected probably aided greatly in the preparation of the pure compound. Also, it was present in quite large amounts in dry leaves, for from one kilogram of dried leaves eight grams of pure chlorophyll may be isolated. The color properties of the pigment as well as its relative abundance are factors which should have made it easy to obtain it in the pure state, but on the other hand the extreme solubility and the ease of alterability of the compound made the task a difficult one, which took many years before the feat was finally accomplished.

I have attempted to give in the preceding part of this paper a brief summary of our knowledge concerning the carotinoids. The chief facts of interest here are that the carotinoids of the plant kingdom are generally believed to be the source of many of the carotinoids found in the animal kingdom; this knowledge has been learned only after many years of experimentation. As yet no direct relation has been discovered between the carotinoids and the vitamines, or in other words the vitamines are probably not carotinoids.

It would be very difficult to say which of the many views regarding the rôle of chlorophyll is the most acceptable one. The general trend of events seems to be that we are coming more and more to accept such views as those of Wiesner. This view holds that chlorophyll is formed and decomposed simultaneously. If such is the case then we are lead to wonder regarding the part that pyrrole plays in the whole process, and also which pyrrole, if any, is the most beneficial.

Can the plant absorb pyrrole as such or does all nitrogen enter it in the commonly accepted way? The relation of nitrogen to the development of chlorophyll is something which has been little stressed in the literature, but can anyone who has worked with nitrogenous fertilizers doubt that there is a direct connection between the green pigment of plants and nitrogen? It seems as if we are coming to learn that the whole process of assimilation is not directly dependent upon chlorophyll, for evidence seems to show that chlorophyll formation is not a limiting factor in plant growth.

Perhaps the only reason that pyrrole compounds have never been found in the soil is that nobody has ever looked for them there. Since many other organic compounds which are present in plants and in animals too have been found in the soil, is there any reason to doubt that pyrrole, which is known to be present in living things in relatively large amounts, will not also be found there? In other words, anything which is present in living things should also be found in the soil, because of the very nature of the origin of the organic part of the soil, unless chemical changes have resulted which decomposed the substances found in living

things. For years we have known and studied every phase of the nitrogen cycle in nature, until we are all quite familiar with this cycle. Is it not worth our time to study pyrrole and seek to know just what part it plays in living cells? Since pyrrole contains nitrogen and is found in blood and in chlorophyll, why should we not study every phase of this problem? At last we have come to the place where we are not contented with the chemist's or the geologist's viewpoint regarding the origin of soil. Soil is something more than mineral matter; it is a very complex body which contains organic as well as inorganic materials, both of which are of great value to the plant, which spreads its roots through the soil in search of food for its metabolic processes.

Another possible relation of chlorophyll shows that in the higher plants the vitamines are localized in the seeds and in green leaves. Maybe we can agree with Mockeridge when she says that there is a vitamine cycle though we may not agree with her explanation of the way things work. At least it is probably true that we will all agree that the entire world obtains its vitamines from plants, even though we may not agree how they are formed in plants. However, the general conclusion seems to be that vitamines are necessary for nearly all plant and animal life.

The exact nature of the vitamines has never been revealed but the evidence seems to show that they may be nitrogen compounds which are cyclic. Many workers are of the opinion that they contain carbon, hydrogen and nitrogen and some even venture to guess that some of the vitamines may be pyrrole compounds. It is my understanding that at the present time the tests for pyrrole compounds are not very definite because many other chemical compounds will also give the pyrrole tests. From what little we already know of pyrrole compounds and their probable relation to vitamines an investigation of the field could probably give us far more knowledge than the present scheme of pyramiding what we already know about the properties of vitamines. The field is one that has taxed the chemist to the utmost, but should be considered by all who are seriously interested in vitamines. The investigation will necessarily have to be a coöperative affair. Maybe now we will agree with Funk that it is best to stop marking time, cease our quibbling and get busy on the real problem and maybe we too can hope with him that the chemical isolation of the vitamines will not be far distant. To discover the rôle of pyrrole in nature, looking forward to the possible finding of a pyrrole cycle, is a problem worthy of the efforts of all who are interested in the biochemistry of living processes.

Maybe by gathering this mass of ideas together we can frame a real story of life that will satisfy each group of us;. agriculturists, biochemists, chemists, soil scientists, plant physiologists, etc. Is not nitrogen—organic and inorganic—taken up by the plant and then found as organic nitrogen in the various parts of the plant? Maybe the inorganic nitrogen goes to form chlorophyll and the organic nitrogen to form other complex nitrogen compounds. Is the chlorophyll—a tetra pyrrole—broken down by light to form various pyrrole bodies which may later function as what we know as vitamines? If such are the facts we might expect vitamines to be found in almost any part of the plant, and so when plant parts are eaten the vitamines pass into the bodies of animals. When these living organisms—plants and animals—decompose, shall not we then find in the humus pyrrole compounds which have been set free from

more complex bodies? Then, in the soil we should expect to find pyrrole compounds and other organic compounds which probably are directly of very great value to growing plants.

Is the story of nitrogen something like this or must we look for a solution of the whole problem at some future date? The problem is too big a one for me to answer, for I have been concerned only with the effect of nitrogen on chlorophyll and know practically nothing regarding the other subjects about which I have written. Final proof will be obtained only after much more work is done, and so I leave the phases of the subject other than chlorophyll to those who possess a far greater working knowledge of the subjects than I do. All I ask is an earnest individual consideration of the whole problem,—Can chlorophyll be broken down chemically by light to form vitamines as nature in her great laboratory is undoubtedly doing every day or are we going to keep on trying to find out what vitamines are in some other way?

LIST OF LITERATURE

In general, only authors' most recent articles are referred to in this bibliography. These will furnish the reader a key to much in the literature. A complete bibliography on chlorophyll, vitamines and the effect of light on chemical compounds would be too lengthy for any paper. In connection with the study of ideas in this paper, references on light, absorption bands and chemical constitution as affected by light should be freely consulted.

Allison, F. E. Nitrogen as a plant food. Jour. Chem. Ed., 3:50–58. 1926.

Amar, Jules. Radiations et chlorophylle. Compt. rend. acad. agr. France, 182:1353–1354. 1926.

Blackman, V. H. Solar radiation and plant growth. Jour. Min. Agr., 33:816–819. 1926.

Cady, H. P. and Robert Taft. Oxidation and reduction. Jour. Phys. Chem., 29:1057–1074. 1925.

Combes, Raoul. Émigration des substances azotées des feuilles vers tiges et les racines des arbres au cours du jaunissement automnal. Rev. Gén. Bot., 38:632–645. 1926.

Coward, K. H. The persistence of vitamine A in plant tissues. Biochem. Jour., 19:500–506. 1925.

Deuber, Carl G. Influence of mineral elements upon development of chloroplast pigments of soy beans. Bot. Gaz., 82:132–153. 1926.

Drummond, J. C., H. J. Channon K. and H. Coward. Studies on the chemical nature of vitamine A. Biochem. Jour., 19:1047–1067. 1925.

Dubosc, A. La chlorophyll et la lumière. Moniteur Sci., 16:228–241. 1926.

Dye, M., O. C. Medlock and J. W. Crist. The association of vitamine A with greenness in plant tissue.—I. The relative vitamine A content of head and leaf lettuce. Jour. Biol. Chem., 74:95–106. 1927.

Eckerson, Sophia H. Protein synthesis in plants. I. Nitrate reduction. Bot. Gaz., 77:377–390. 1924.

Funk, Casimir. The Vitamines. 1922.

Gibson, R. J. Harvey. A photoelectric theory of photosynthesis. Ann. Bot., 22:117–120. 1908.

Javillier, M., P. Baude and S. Lévy-Lajeunesse. Essais d'identification du facteur A. Le facteur A et le phytol. Compt. rend., 179:998–1000. 1924.

Lasareff, P. Über die Absorption des Lichtes durch die Blätter der Pflanzen und die Absorption von Chlorophyllösungen. Biochem. Z., 182:131–133. 1927.

Lubimenko, V. Les pigments des plastes et leur transformation dans les tissus vivants de la plante. Rev. Gén. de Bot., 40:23–29. 1928.

Mockeridge, Florence A. The formation of plant growth-promoting substances by microorganisms. Ann. Bot., 38:723–734. 1924.

Morhardt, P. E. The chemical constitution of vitamines. La Nature. No. 2771. p. 276. 1927.

Noack, Kurt. Photochemische Wirkungen des Chlorophylls. Naturwissenschaften, 14:383–389. 1926.

Oddo, B., and G. Pollacci. Influenza del nucleo pirrolico nella formazione della chlorofilla. Gaz. chim. Ital., 50:54–70. 1920.

Palmer, Leroy S. Carotinoids and Related Pigments. 316 pp. 1922.

Randoin, L., and H. Simonnet. Essai de définition des vitamines. Bull. Soc. de Chim. Biol., 7: 1020–1023. 1925.

RENTZ, EDVARD. Some investigations into the pharmacodynamic properties of chlorophyll. Upsala Läkarefören Förhandl. N. F. Vol. 33: 371–392. 1927.

SEIDELL, ATHERTON. Concentrated antineuritic vitamine prepared from brewers' yeast. Jour. Biol. Chem., 67:593–600. 1926.

SCHERTZ, FRANK M. Commercial applications of chlorophyll derivatives. Jour. Ind. and Eng. Chem., 19:1152. 1927.

———. The effect of potash, nitrate and phosphate, upon the chloroplast pigments, upon the mineral content of the leaves and upon production in crop plants. In press.

SCHREINER, OSWALD, and J. J. SKINNER. Nitrogenous soil constituents and their bearing on soil fertility. Bureau of Soils Bulletin. No. 87. 1912.

SHERMAN, H. C., and S. L. SMITH. The Vitamins. 1922.

SPOEHR, H. A. Photosynthesis. 393 pp. 1926.

STEENBOCK, H., and K. H. COWARD. Fat-soluble vitamines. XXVII. The quantitative determination of vitamine A. Jour. Biol. Chem., 72: 765–779. 1927.

ULLRICH, HERMANN. Die Rolle der Chloroplasten bei der Eiweissbildung in den grünen Pflanzen. Zeitschr. f. Botan., 16:513–562. 1924.

WILLSTÄTTER, RICHARD, and ARTHUR STOLL. Translation by Schertz, Frank M. and Albert P. Merz. Investigations on Chlorophyll. 385 pp. 1928.

WLODEK, JEAN. The spectrum of chlorophyll in the living leaf. Bull. Acad. Sci. Cracovie, 5–6 B: 407–423. 1925.

WOLFE, H. S. The auximone question. Bot. Gaz., 81:228–231. 1926.

WURMSER, RENÉ. Le rendement énergétique de la photosynthèse chlorophyllienne. Ann. Physiol. et Physicochem. Biol., 1:47–63. 1925.

ZIRKLE, CONWAY. The structure of the chloroplasts in certain higher plants. Amer. Jour. Bot., 13: 301–341. 1926.

THE DEVELOPMENT OF MODERN COMPARATIVE PSYCHOLOGY

By C. J. WARDEN

Animal Laboratory, Department of Psychology, Columbia University

FROM the very earliest times man has interested himself in the life and behavior of infra-human organisms. Among the ancients, Aristotle (384–322 B.C.) was the first to attempt a systematic account of plant and animal behavior and it is significant that he included in his natural history description the psychological aspects of the organism. In his *De Anima*, *Historia Animalium* and related writings he has brought together the results of his own extensive observations supplemented with the winnowings of the animal lore of earlier times. Aristotle very justly deserves to be considered the father of comparative psychology, as well as the founder of the other biological sciences and of natural history in general. His emphasis upon observation and the inductive method and his tacit adoption of a broadly comparative viewpoint mark his work as monumental in the early history of natural science. His conception of the organism was vitalistic in agreement with his general philosophical position, and his interpretations of behavior were teleological and often naïvely anthropomorphic. His work was marred also by an extensive use of anecdotal material to supplement original observation. Nevertheless, his contribution to the general development of biology and of comparative psychology was hardly equalled by any other writer previous to Darwin.

The interest in natural history rapidly declined after Aristotle. Later Greek and Roman writers turned from the study of nature to metaphysical and ethical speculation in the main, while a few like Pliny (23–79 A.D.) and Plutarch (c. 46–120 A.D.) became mere compilers of anecdotes illustrating the sagacity of the higher animals. During the early centuries of the Christian era the normal interest of mankind in natural science was displaced to a large extent by religious activities and theological speculation. Pliny was widely read, but the biological and psychological writings of Aristotle were generally unknown, ignored, or even proscribed in Christian lands.

The revival of the natural history writings of Aristotle in Christendom about the middle of the thirteenth century marked the beginning of an important advance in the field of biology. This came about very largely through the influence of Albertus Magnus, Thomas Aquinas, and such contemporary encyclopedists as Vincent of Beauvais, Bartholomew Anglicus and Thomas of Cantimpré. Unfortunately it was the body of facts contained in the writings of Aristotle rather than the scientific spirit of the Stagirite that was revived at this time. His works on natural history and psychology, interpreted by orthodox scholars, became a new source of authority instead of an inspiration to further observation of nature. The major interest seems to have centered around the problem of the essen-

tial difference between the mental life of man and animal. Some solution to this problem appeared necessary in the interests of a rational theology. The animal is guided by blind, impulsive instinct, divinely implanted, according to the orthodox writers of the time, while man is a rational being, distinguished by the capacity for voluntary activity involving moral and spiritual responsibility.

The revival of the spirit and method of Aristotle in the field of natural history came about as a part of the scientific renaissance of the sixteenth century. The *Historia Animalium* of Gesner, the famous Swiss naturalist, which began to appear in 1551, and the more specialized works of such contemporary naturalists as Belon, Rondolet and Turner mark the beginnings of the new movement which finally led to the replacement of armchair compilation by original observations of animal life and behavior. The three centuries extending from Vesalius to Darwin were crowded with discoveries and new developments in the field of biology. The invention of the microscope, about the opening of the seventeenth century, broadened the realm to include the hitherto unknown microorganisms, and made possible the marvellously detailed study of insect structure which characterized the work of Réaumur and his school. Notable contributions were also made by this group in the field of behavior. The study of the structure and function of plants and animals became more and more specialized, and the old natural history was gradually broken up into the major biological subsciences as we know them today. Up to the time of Darwin infra-human behavior was more or less ignored by the leading biologists in favor of taxonomical, morphological, physiological and embryological investigations, although the naturalists and explorers of the preceding century contributed an extensive literature of field observations that is not wholly without value. Questions relating directly to the nature of animal mind and behavior engaged the attention mainly of the philosopher, or of the scientist in the rôle of philosopher. The well known view of Descartes (1596–1650) and his followers that even the higher animal is merely an automaton (*la bête machine*) contrasts sharply with contemporary vitalistic and anthropomorphic tendencies, while both, insofar as they recognized the primacy of man, were in general agreement with the orthodox view which had come down from the middle ages.

In a very important sense Darwin may be considered the founder of modern comparative psychology. The publication of *The Origin of Species* (1859) brought the problem of mental evolution to the fore and stimulated a widespread and lasting interest in the mental life and behavior of infra-human organisms along broadly comparative lines. As we shall see, the natural development of this interest into a well-balanced and systematic science was held in check for several decades by the controversial aspects of the evolutionary doctrine. After Darwin, however, psychology began very properly to consider itself a division of biology rather than of philosophy, to divest itself of metaphysical and mentalistic categories and to broaden its scope to include more and more the entire infra-human field. The movement has taken on the aspects of a young but rapidly growing natural science during the last quarter century, especially in America, where the conditions for development have been most favorable. At the present time comparative psychology may justly lay claim to separate status as a biological discipline corresponding in general scope to the older

sciences of comparative anatomy and comparative physiology. It has firmly established itself in a more or less clearly defined field with its own systematic problems and its own experimental methodology.

An account will now be given of the more important developments from the time of Darwin onward grouped according to the following outline:

I. The Anecdotal Period (1859–c. 1890)

1. The influence of Darwin
2. The anecdotal movement
3. Contemporary scientific contributions

II. The Experimental Period (c. 1890–)

1. Beginnings of the movement
2. Experimental developments
3. Theoretical tendencies

THE ANECDOTAL PERIOD

The influence of Darwin

Although modern comparative psychology took its rise from the evolutionary movement initiated by Darwin, it gave little promise of developing into a systematic science until about the beginning of the last decade of the nineteenth century. In the meantime, it suffered along with biology in general from the strong opposition which the traditional science and theology offered to the evolutionary hypothesis. The early interest lay almost wholly in a defense of the notion of mental continuity. So long as attention was being directed chiefly to the more controversial aspects of Darwin's view a normal development along well-balanced and experimental lines could hardly be expected. The anecdotal school arose as the first and most direct result of the influence of Darwin. These early workers felt called upon to hold a brief for human-like mental traits in the higher animals. In the absence of better evidence at hand they made a most unwarranted and extravagant use of anecdote, supplemented at best by casual observations of the natural history type.

Like his great predecessor Aristotle, Darwin was primarily a naturalist in the broadest sense rather than a psychologist. He was not well versed in traditional psychology and had little or no acquaintance with contemporary thought in this field. He dealt with psychological problems only insofar as they came within the province of his larger interest in biological evolution. We are not surprised, therefore, to find him accepting in an uncritical manner the terminology of the popular psychology of his day. In his treatment of the mental life of animals he was naïvely anthropomorphic in much the same vein as Aristotle and made much the same conservative use of anecdote. Nevertheless, it is almost impossible to overestimate the influence of his genius on the general field of psychology. The evolutionary concept gave unity and meaning to such disconnected facts as had been accumulated, and led in time to an extensive use of the genetic method and to the functional *vs.* structural interpretation of psychological phenomena.

The view of Darwin that "the mental faculties of man and the lower animals do not differ in kind, though immensely in degree" was highly revolutionary in nature. Orthodox science as well as orthodox theology still held tenaciously to the Hebrew cosmology and insisted upon the immutability of species. And this, in spite of the evolutionary teachings of Buffon, Lamarck and many of the leading philosophers of the preceding century. Moreover, the conception prevailed that the mental life of infra-human organisms could be summed up in the term instinct—a biological faculty, or a mysterious entity constituting the primal psychical endowment of a beneficent

1. Charles Darwin, 1809–82; *Harcourt portraits of scientists.* 2. G. J. Romanes, 1848–94; *Open Court Pub. Co., Chicago.* 3. Sir John Lubbock, 1834–1913; *from a photograph.* 4. C. Lloyd Morgan, 1852– ; *Open Court Pub. Co., Chicago.* 5. Max Verworn, 1863–1921; *from a photograph.* 6. Jacques Loeb, 1859–1924; *C. H. Stoelting Co., Chicago.*

creator. Man, as the sole possessor of the faculty of reason, was sharply marked off from even the higher animals on the mental side. This view was, of course, nothing more or less than the qualitative dichotomy between man and brute that had survived from the middle ages. The Darwinian assumption of physical and mental continuity within the organic world, and the serious attempt to account for both along broad genetic lines aroused bitter and determined opposition on all sides.

The evolutionary conception, regardless of its specific formulation, brought with it several problems of great interest to comparative psychology. First, there was the question as to the origin of mind comparable to that regarding the origin of life in biology. On this point Darwin had nothing to say on the positive side. "I have nothing to do with the origin of the mental powers," he writes, "any more than I have with life itself. We are concerned only with the diversities of instinct and of the other mental faculties of animals of the same class." (29, I:319). Given life and mind, or living organisms with a mental endowment, he concerned himself with the evolution of complex and varied types from the simple and unitary. A second problem, and the fundamental one, for Darwin, related to the factors which may have operated in the several stages of organic, including mental evolution. And since instinct and intelligence were generally considered to be essentially different mental types the development of both had to be accounted for.

A half century previous to the publication of *The Origin of Species*, Lamarck (63) had attempted to show the *modus operandi* of the development of the instincts on a naturalistic basis. The explanatory principle of Lamarck was later elaborated by Spencer, among others, and called by him the "lapsed intelligence theory." Lamarck held, in brief, that use and disuse of various parts, or members of the organism brought about more or less definite, local changes which were transmitted from generation to generation. He did not deny the influence of the direct effect of environment (Buffon's principle) but stressed functioning (use and disuse of parts) as the all-important factor, and he included conscious as well as purely physiological functioning. It is the desire of the giraffe to feed on higher foliage, accompanied by the stretching of the neck, for countless generations, as the expression of that desire, that finally brought about the development of the unusually long neck. Instinctive patterns have been developed *pari passu* with morphological change; habitual responses initiated by conscious desire, or some form of internal or psychic urge, have been passed on as a cumulative heritage and finally fixated in the species as instincts. Lamarck's view is obviously meaningless apart from the generally discarded theory of the heritability of acquired morphological and functional changes in the organism.

Darwin appealed in the main to the principle of natural selection to account for the evolution of instincts and of mental life in general. He did not deny the operation of other factors, such as those previously applied by Buffon and Lamarck, but he considered these relatively unimportant, and as merely supplementary to his own principle of selection. Functional types, like structural types, had been evolved by the gradual accumulation of favorable variations in the struggle of the organism to survive. The more complex and elaborate instincts had developed gradually out of the less complex, and these in turn out of still simpler.

He says: "If it can be shown that instincts do vary ever so little, then I can see no difficulty in natural selection preserving and continually accumulating variations of instinct to any extent that was profitable. It is thus, as I believe, that all the most complex and wonderful instincts have originated." (29, I:321).

The evolution of intelligence was explained on precisely the same basis—variation, natural selection and heredity. Darwin considered it absurd to deny a low order of intelligence, including imagination, reason and will, to many of the higher animals. He believed implicitly that the mind of man with all its wealth of emotional life and its moral sense had developed naturally out of the mind of the higher animals possessing these same attributes in a rudimentary way. In *The Descent of Man*, and in *The Expression of the Emotions*, originally planned as a chapter of this treatise, he attempted to illustrate his own conception of how this development had actually taken place.

In his opinion, the conscience and the moral sense constituted the greatest practical difference between man and the higher animals. With keen insight he perceived that insofar as these were actually possessed by man they were the natural accompaniment of his highly developed intellectual and social life. It seems highly probable, so he says, that "any animal whatever, endowed with well marked social instincts, would inevitably acquire a moral sense or conscience, as soon as its intellectual powers had become as well developed, or nearly as well developed, as in man." (30, I:68).

In accounting for the development of complex mental functions and moral attributes Darwin applies the principle of natural selection very broadly, placing great emphasis upon the operation of process. In a state of nature, perhaps, selection may tend to the preservation of one individual against another, but as soon as the social instincts arise the preservation of the group becomes the chief end to be attained. Utility to the group, as well as mere individual strength and endurance, becomes a factor in survival. Sympathy, mutual aid, parental and filial affection, and other social behavior as well as individual cunning, discrimination capacity, etc., operate as increasingly important determinants of the course of evolution among the higher animals. In man himself, the use of fire, traps, tools, weapons, signs, language, etc. are instances of how intelligent behavior, making for group solidarity and social organization, may dominate the evolutionary trend.

The anecdotal movement

Although Darwin did not make an explicit application of his theory to man in the first publication of his views in *The Origin of Species*, the point was sensed immediately that man must be included in any thoroughgoing evolutionary scheme. The full implications of the theory, as Wallace phrases them, were "that man's entire nature and all his faculties, whether intellectual, moral or spiritual, have been derived from their rudiments in the lower animals, in the same manner and by the action of the same general laws as his physical structure has been derived." (88, page 461). Even such ardent supporters of the theory of organic evolution as Huxley (59, 60) and Wallace (88) did not accept completely the views of Darwin, above expressed, concerning the mental evolution of man. They insisted that certain of the higher mental faculties, and particularly the moral and spiritual capacities, could not be accounted for on Darwinian principles.

inclusive of the *genus homo* thus became the storm center of the whole controversy over Darwinism. The notion that mind as well as bodily structure and function had developed from natural causes amounted to a denial of the primacy of man in any but a purely quantitative and naturalistic sense. The mind-body dichotomy was rather clear cut in the public mind because of the fact that the philosophic thought of the time was more or less permeated by Cartesian dualism. The bitter attacks of theologians and religious leaders, who thought they saw in the new doctrine the collapse of moral culture and religious faith, added tenseness to the situation. It was this stubborn refusal on all sides to accept the fact of mental evolution, insofar as it applied to man, that was in large part responsible for the anecdotal movement in comparative psychology.

The anecdotalists confined their efforts almost wholly to the collection of stories, sometimes of doubtful veracity, emphasizing the human-like behavior of the higher animals. The lower organisms were of slight interest since the traditional science and theology had placed the impassable gap to mental continuity between the higher animals and man. The problem thus practically narrowed down to showing that the higher animals possessed a rudimentary intelligence, out of which the more diversified human mental life might conceivably have developed. The need of the hour, if the doctrine of mental continuity and evolution were to survive, was for a mass of concrete evidence, tending to show the beginnings of rational, emotional, social and moral capacities in the higher animals. In the absence of first hand observations, appeal was had to the anecdote, which had always been in good repute in illustrating unusual conduct in animals in natural history collections.

Darwin himself made considerable use of anecdote and few if any of the writers on natural history of this period avoided it altogether. Scores of anecdotal collections appeared in which the tendency to humanize and eulogize the mental powers of higher animals reached the ridiculous. These collections often included material from Aristotle, Pliny, Plutarch and other of the ancients in addition to that gathered from contemporary story-mongers. In many cases the anecdotes were taken from unreliable sources or were mere hearsay, and in all cases the moral to the story was that the animal concerned was "almost human" if not actually so. The collections of Romanes (74, 75, 77), Büchner (26), Lindsay (66) and Perty (70) are among the most extensive and dependable of those which have survived to our own day. Romanes in particular attempted to select his stories with due concern as to the reliability of the original sources.

The essential argument in much of the anecdotal material is difficult to follow on account of the loose manner in which fact and fancy are thrown together. In general, however, the anecdotes may be grouped so as to constitute the following three main lines of evidence in support of the contention that the higher animals possess a rudimentary human mind: (1) anecdotes purporting to show some measure of reasoning ability, (2) anecdotes supposedly illustrating social behavior of a high order, and (3) anecdotes in which the characteristic human emotions indicative of sympathy, shame, deceit, courage, timidity, suspicion, jealousy, curiosity, emulation, sense of justice, sense of humor, etc. are apparently exhibited. Cunning and ingenuity in the natural environment such as that shown by the beaver in building its dam at strategic positions, or in domestic and captive animals in outwitting man, or learning tricks with or without tuition

would properly belong in Class 1. Imitation, purposive coöperation, intercommunication of ideas and plans of action by means of signs, or sounds that serve the language function would fall in Class 2. The fallacy of anthropomorphic analogy reached its worst in the fanciful interpretations of Class 3, the underlying assumption seeming to be that if the animal acts like man it also feels like man.

The following criticisms may be urged against the anecdote as a source of scientific information regarding the mental life and behavior of animals: (1) that the observer is likely to be untrained and unable to give an accurate account of the happening, even if his intentions are of the best; (2) that interpretative elements are likely to be confused in the report with factual, making it impossible for the scientist later to separate the two; (3) that the happening even when adequately reported is usually an incident cut off from the essential genetic antecedents (both individual and phyletic) which would explain it and give it proper significance; (4) that the happening, in the nature of the case, represents highly selected and atypical behavior that can have little or no statistical validity; (5) that even if the tendency of mankind to humanize the animal—whether in a scientific or a literary mood—is restrained, errors of memory and of transmission (if verbal) are likely to enter; and (6) there is the difficulty of selecting reliable, authentic material from the various available sources. It is evident that the method, even when guardedly employed, which usually is not the case, hardly deserves to be considered scientific in the strict sense.

The anecdotal collections were widely read and the popular imagination was deeply stirred. In fact, the wide appeal to anecdote by the protagonists of the doctrine of mental evolution was not altogether without value as a reaction against the older instinct-reason antithesis. Just as philosopher and theologian had previously twisted the facts in order to create an insuperable gulf between the mind of man and animal, so now by the opposite bias that gulf was not only bridged, but the difference between the mind of man and animal unduly minimized—owing in large part to the controversial temper of the times. The general acceptance of the view of Darwin that the entire mental life of man must be included in the general scheme of mental evolution made the appeal to anecdote no longer necessary or excusable.

Anecdotalism and anthropomorphism at the level of Pliny and Plutarch shared honors with specious reasoning and far-flung analogy. The natural philosophers were obsessed with pedantic attempts to achieve a monistic *Weltanschauung* regardless of fact or logic—a natural reaction, engendered by the general evolutionary movement, against the current dualism. The cell-soul theory of Haeckel (50) and the psychade theory of Schultze (51) are examples of the type of speculation which sought to find in each living cell a psychic substrate or attribute, usually held to be below the conscious level but analogous to mind in higher organisms. Serious consideration was given to such fanciful discussions of plant life as appears in Fechner's *Nanna* (1848) and contemporary writings of the same sort.

The notion that ontogeny repeats phylogeny in mental development was applied very literally, especially with respect to man himself. The classic example is the psychogenetic scale worked out by Romanes and elaborated in his *Mental Evolution in Animals*, and in the companion volume on the mental evolution of man. He compares in great detail the mental status of the embryonic and early

developmental stages of the human with the mental levels of the various phyla of the animal kingdom as these were supposedly revealed by the anecdotal evidence at hand. At birth the human infant has reached the mental level of the echinodermata. Some twelve successively higher stages are then recapitulated before the fifteenth month, at which time the mental level of the dog and the anthropoid ape has been reached. Romanes seems to have considered his psychogenetic scale as a scientific application of the principle of mental continuity, and so it was looked upon by many of the foremost thinkers of the time.

Contemporary scientific contributions

Fortunately, not all of the interest aroused in comparative psychology was absorbed in fruitless speculation or in collecting anecdotes. Original observations of plant and animal behavior were being made constantly during the period and many of these have proven to be of genuine value. The naturalists made a worthy contribution to our knowledge of animal life and behavior under natural environmental conditions. There was a marked tendency for field studies to become more and more intensive and precise. In fact the observation of the period, at its best, often approached and sometimes attained the experimental level. Important developments in the related fields of comparative anatomy and comparative physiology made available a wealth of fundamental facts that were necessary before genuine progress in comparative psychology could be made. The structure and function of the sense-organs and nervous system of the lower forms in particular were studied extensively by many of the leading biologists of the day. The findings in these fields usually involve behavior data of a more or less simple sort, and no attempt will be made to distinguish between the contributions of anatomist, physiologist, naturalist and psychologist in the following discussion.

The works of Darwin, Wallace, Hudson, Houzeau, Bates and Belt are examples of the better and more comprehensive general field studies. As will be noted, these deal in large part with the relatively unknown fauna of various countries covered by scientific expeditions. The volume of Hartmann on anthropoid apes, of Espinas on the social life of animals, and of Poulton on animal coloration are important illustrations of field studies of more limited extent. The classic natural history of the period was Brehm's *Thierleben*, which occupied much the same position in the nineteenth century as the *Histoire Naturelle* of Buffon had in the preceding century.

Except for anatomical-physiological investigations the vertebrates were relatively neglected aside from field studies of the type indicated above. It was decidedly easier to gather anecdotes than to make careful and long continued observations at close range and naturally the birds and higher mammals were especially favored with anecdotal lore. Rarely does one find in the literature of the period covering infra-human vertebrates a study at once as intensive and as comprehensive as that of Kussmaul (62) or Darwin (34) on the human infant or that of Preyer (72) on the human child. The report of Romanes and his sister (74, 483–498) on the cebus monkey and that of Spaulding (83, 84) on birds are among the better class of first hand observations made at close range on higher forms during this period.

Much more serious work was attempted on various classes of the invertebrates. Binet (24) has given us a good account of investigations on the behavior of the protista previous to the epoch making

Protisten-studien of Verworn (1889). He argues, on the theoretical side, for a psychic *vs.* a purely physico-chemical explanation of the multiform activities of unicellular organisms. The volume of Romanes (76) describing his experiments on jelly-fish, star-fish, and sea-urchins contrasts sharply with his anecdotal and theoretical treatises. Preyer's experimental study of the starfish deserves special mention, as well as Darwin's volume on the earthworm. Our knowledge of the behavior of the lower invertebrates was greatly enriched by the careful investigations of a large number of biologists working along various lines. An impressive list of names might be given which would include O. Hertwig, R. Hertwig, Gegenbauer, M. Schultze, Lankester, Haeckel, Mach, Plauteau, Delage, J. Massart, Engelmann, Bert, Graber, and Merejkowsky as well as many others.

The arthropoda, and the insects in particular, were especially singled out for study by anatomist, physiologist and naturalist alike. The interest aroused in insect life by Réaumur and his school during the latter half of the eighteenth century was continued into the present period by Straus-Durkheim, Newport, Leydig, Kraepelin and others. The naturalist Fabre (40, 41) made a most extensive series of observations on insect life over a period of more than forty years. Among the many workers who might be named, Wasmann, Forel, Claparède, Eimer, Emery, McCook, Huber, and Graber deserve mention. The earlier work of Lubbock and of the Peckhams (69) also properly belongs to this period. The work of these investigators differed widely in quality and in some instances had little permanent value. The naturalists showed their usual tendency toward anthropomorphism and it is not always easy to separate the element of fact from the interpretative statement of the observation.

The writings of Fabre, "that inimitable observer," as Darwin called him, are especially open to criticism. His theological bias unquestionably led him to grossly exaggerate the uniformity of insect behavior and many of his findings have been shown to be unreliable by later and more dependable observers. In his zeal to uphold the instinct-reason dichotomy as separating man and beast he strenuously opposed Darwinism, and argued for the mediaeval conception of instinct as the original endowment of the creator. Animal instinct was to him an irresistible inborn impulse, always routine and uniform—albeit an "inspiration" which at its best might even simulate intelligence or reason. He was strongly opposed to physicochemical explanations of insect behavior and reported his findings in anthropomorphic language that would have done credit to an anecdotalist of the extreme evolutionary school. He finds in instinct—an eternally inscrutable faculty—the answer to every problem that arises in connection with the behavior of insects, and indulges in flights of fancy that betray a literary rather than a scientific imagination. The theological viewpoint of Fabre is shared by the well-known entomologist, E. Wasmann, S. J., who in our own day has written a large volume (89) against the theory of evolution. In this and other of his writings he argues for the instinct-reason dichotomy, although his observations, unlike those of Fabre, are held in high esteem by present day entomologists. He holds that the evolutionary psychology, by denying the essential difference between the mind of man and animal "not only raises brutes to the dignity of man, but degrades man to

the level of the brute," the practical consequences being "the demoralisation and brutalisation of man."

Important developments took place during this period in the field of plant behavior (47, 53). The term tropism had been introduced by the botanist DeCondolle as early as 1835 and long before this Knight (1805) had shown the effect of gravitation on the direction of growth in seedlings. Aside from the work of Darwin and F. Darwin, which will be discussed at some length below, valuable contributions to the behavior aspect of plant life were made by Sachs, Pfeffer, Strasburger, Weisner, Stahl and many other botanists of the period. Plant behavior was usually thought of as being purely physiological and as lying entirely outside the pale of psychology and hence it escaped for the most part the evil influence of anecdote and anthropomorphism.

Darwin himself gave no little time to the experimental investigation of various phases of plant life. His earlier interest was largely confined to morphological variation under domestication as an instance of the evolutionary principle, and to such related topics as fertilization and sexual dimorphism. However, he later took up the problem of plant behavior, and in 1875 published a volume on climbing plants and one on insectivorous plants, the latter attracting wide attention because of the novelty of the material.

Darwin's most notable contribution to the study of plant behavior was *The Power of Movement in Plants*, written in collaboration with his son, Francis, and published two years before his death. The book is replete with simple but ingenious experimental methods, some of which have become classic, and with results interpreted more often than not with rare insight. Darwin found that practically all parts of the plant—stems, leaves, roots, flowers, etc.—normally perform circumnutation movements even when shielded from external stimulation. From this general fact he was led to believe that all tropistic responses of plants were merely variations of this inner power of movement directed in part by such external energies as gravity, light, pressure, etc. He was among the first to recognize special sensitive zones such as tip of root and shoot, transmission of excitation through the tissues to point of curvature, and the general similarity of plant and animal behavior in its more fundamental aspects. The tip of the radicle, which exhibits a multiform sensitivity in penetrating the ground, seemed to him to act "like the brain of one of the lower animals" in directing the general movement of the root.

The contribution of the anecdotalists was relatively insignificant in comparison with that of these various groups of workers who, in one manner or another, were making direct observations of plant and animal behavior. At best the anecdotal material served only a temporary purpose in connection with the controversy over the mental evolution of man. Furthermore, the anecdotalist movement was a positive evil insofar as its influence tended to retard scientific investigation of the behavior of the higher animals. The observation of the naturalist and the more careful studies of anatomist and physiologist, insofar as their findings were relevant, represent the more permanent contribution of the period to comparative psychology.

THE EXPERIMENTAL PERIOD

Beginnings of the movement

Although Darwin stands apart as the great pioneer spirit in the rise of modern

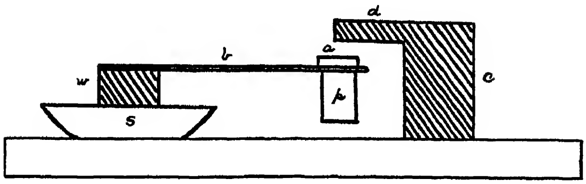
comparative psychology both he and his immediate successors—the anecdotalists—confined their attention largely to the problem of psychogenesis and made no serious attempt to develop the science along systematic lines. The behavior material which various groups of biological workers gathered from time to time in connection with anatomical, physiological or naturalistic studies was ignored, for the most part, by contemporary psychologists or distorted by anthropomorphic interpretation. Not until about 1890, when we come to the work of Lubbock, Verworn, Loeb and C. Lloyd Morgan, do we find the movement giving definite promise of developing into a systematic biological science. In fact these four men may be considered the outstanding leaders in the reform that ushered in the new epoch.

The new movement began as a revolt against both the viewpoint and the method of the earlier post-Darwinian period. The humanizing tendency, when given free rein, had gone to such absurd lengths as to make a reaction inevitable in the interests of a common sense sanity. The anecdotal method, as the handmaid of extreme anthropomorphism, could hardly hope to survive after the general acceptance of the doctrine of mental evolution, although for a time it had seriously threatened the normal development of observational and experimental methods. The new movement, as we shall see, was characterized by (1) the use of greater precision in observation with a growing emphasis upon carefully controlled experiments of the laboratory type and (2) a more critical use of anthropomorphic analogy, which led in time to a rejection of it altogether in favor of a strictly objective or behavioristic position.

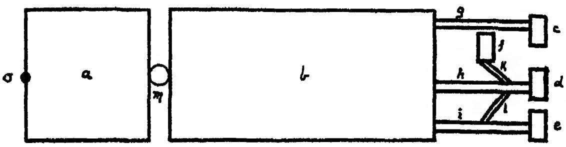
On the basis of initial important contribution, Lubbock, the English naturalist, antedates the other members of the group by almost a decade, his experimental studies on insect behavior appearing in collected form in 1882. In a sense he and Morgan represent the direct line of conservative leadership in comparative psychology following Darwin, Romanes and others of the anecdotal period. Both Lubbock and Morgan were stoutly opposed to the use of anecdote and extremely cautious in appealing to anthropomorphic analogy. Lubbock's importance in this historical connection rests primarily, as we shall see, upon his priority in the application of experimental technique to behavior problems. His work was practically complete when Morgan began to come into prominence, although his direct influence on laboratory methods (211) extended well into the present century.

In attempting to evaluate the contribution of each of the four outstanding leaders to the new movement the work of Verworn and Loeb on the lower organisms may be conveniently treated together. Both of these eminent physiologists, even in their earlier work, which chiefly concerns us here, devoted themselves to observational and experimental methods of a relatively high order, and both attempted to give a strictly objective account of the activities investigated. Although Verworn antedates Loeb somewhat, the influence of the latter was more widely felt because of the important controversy aroused by his radical tropism theory.

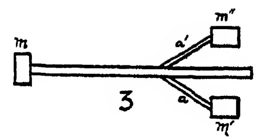
The pioneer experimental studies of Lubbock on insects mark him as the founder of the modern laboratory method of approach. This work, which had occupied him for many years, was brought together in his earlier volume (166) in 1882. He seems to have originated the maze method, making first use of the now

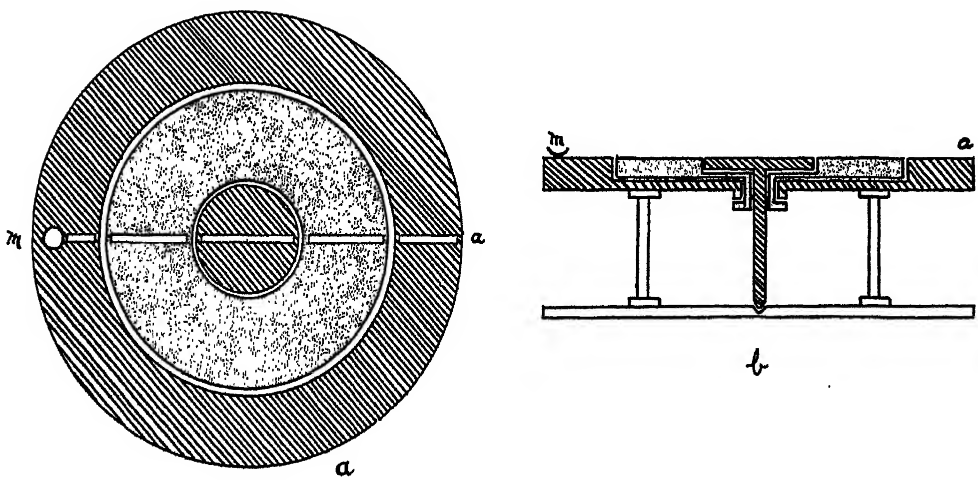


1



2





4

SPECIMENS OF APPARATUS DEVISED BY LUBBOCK

FIG. 1. *Simple Problem Apparatus.* The insect could secure access to the larvae in the glass cell, *p*, only by climbing onto the wooden block, *c–d*, and dropping 0.3 in. at *a*: the wooden block, *w*, rested in a saucer of water.

FIG. 2. *Complex Insect Maze.* The insect passed from the nest, *a*, to the board, *b*, 2 feet long, and approached the maze, consisting of paper strips, *g–h–i*, leading to larvae or food on the glass slides, *c–d–e*; movable pathways, *k–l*, with slide, *f*, complicated the pattern.

FIG. 3. *Simple Elevated Insect Maze.* Larvae placed on columns, *m–m'–m''*, 7 in. high, could be reached by traversing the paper pathways supported on pins.

FIG. 4. *Complex Problem Apparatus (Top and Horizontal Sections).* By means of this rotating table, 18 in. in diameter, devised for Lubbock by Francis Galton, the trail leading to larvae or food at *m* could be shifted at various points; environment could be rotated with trail by placing a round box, or hood over the rotated section.

standard *Y* type, the elevated insect maze, and various irregular patterns which he employed extensively in connection with his studies on the sensory capacities of the ant. To him should go the credit also for first making definite use of the puzzle device or problem method under laboratory conditions. He constructed his varied problem apparatus upon the principle that the best way to test animal intelligence is "to interpose some obstacle which a little ingenuity would enable them to overcome" between animals and such natural incentives as food, the young, freedom, etc. Although the various devices of Lubbock were especially adapted to insect manipulation, this principle is the fundamental one involved in most later types of problem apparatus (211) as used for all sorts of animals. Lubbock not only originated two of our most important general laboratory methods—maze and problem situation—but also invented a most ingenious glass-covered nest for ants in which he kept some groups under continuous observation, under fairly normal living conditions, for over seven years. He claims to have been the first to mark particular ants and record their individual behavior on an extensive scale. He checked up by his more exact methods the conclusions of earlier and contemporary observers of insect life and showed that the current anthropomorphic interpretations in this field were usually based upon careless or insufficient observation. His own results, arranged in tabular form, appear modern indeed in comparison with the reports of most other naturalists of the time.

Lubbock made extensive use of the "preference method" in his study of the visual range, color vision, and other sensory capacities of insects, but he adopted a critical attitude in the matter of interpreting his findings. The preference method had been used earlier by Bert, Graber (135) and others in attempting to determine discrimination ability in various types of invertebrates. As commonly employed in color vision work, the animals to be tested were equally distributed over the floor of a long narrow box covered with colored glass arranged in spectral order. Withdrawal from, or collection in a given section—under a given colored glass—was usually interpreted to mean not merely differential sensitivity, but genuine preference based upon pleasure-pain or even aesthetic factors. Lubbock insisted that the method showed no more than differential sensitivity and explicitly denied that sensitivity to wave length as thus induced in an insect or other animal meant sensations possessing the characteristic human quality. That is, we cannot argue that an object that appears red to a normal human being likewise appears red to the sensitive animal.

In his later volume (167) Lubbock made the first serious attempt to cover the field of comparative psychology without recourse to the prevailing anecdotal literature. He drew his facts mainly from the anatomists and physiologists, and with due caution from the naturalists—the very sources indeed that the anecdotalists in general ignored. The first ten chapters deal with the sensory capacities of animals, including man, the three following chapters are devoted to his favorite topic—the instincts and intelligence of insects, while the final chapter on the dog includes mainly a report of his experiments on his own dog, Van. That he preferred to leave the treatment of the higher animals thus incomplete rather than resort to anecdotal evidence indicates the depth of his devotion to scientific fact. In introducing laboratory methods into

comparative psychology and in taking in general an objective attitude in matters of interpretation he showed himself to be several decades ahead of his time.

The early work of Verworn (217) and of Loeb (161) on the lower organisms was a continuation of that of the botanists, anatomists, physiologists and zoologists of the preceding period. Following the excellent work of Engelmann (127, 128) and others, Verworn carried out the most thoroughgoing investigation of unicellular forms that had been made up to that time. His experimental findings were brought together in the *Protisten-studien* (1889), which occupied much the same position then as the well known volume of Jennings (149) does at present. Verworn emphasized the apparently spontaneous, or internally stimulated activity of unicellular forms, while insisting upon a physico-chemical explanation of their behavior. It is true that he indulges in speculation which suggests the influence of Haeckel's monism, but this is entirely absent in his later volume (1894). Here (218) he gives a clearer and more straightforward statement of his tropism theory and of his general view regarding the nature of the behavior of organisms. He differed from the more radical position of Loeb in much the same way that Jennings, his pupil, came to differ later.

Loeb began his work on the plant-like, sessile Coelenterates and was the first to make extensive use in the analysis of animal behavior of technique similar to that developed earlier by the botanists. Taking his cue from the tropism studies of the plant physiologists, he attempted to determine to what extent the orientation responses of lower animals to external stimuli could be described and explained on a similar basis. He was led to the conclusion that most, if not all, of the behavior of lower animals was tropistic in much the same sense as that of plants, and therefore unconscious. The physico-chemical explanation of Loeb was new and startling, primarily because of his insistence that lower organisms react wholly on the non-psychic level. This point was generally conceded insofar as the plant kingdom was concerned—fortunately the anecdotalist and the philosopher had, in the main, kept aloof from the lowly plant.

The new view, and particularly the tropism theory of Loeb, was little short of a complete return to the mechanistic position of Descartes, and came as a fatal shock to the post-Darwinian humanizers. This bold attempt to analyze the behavior of lower organisms by physiological methods and to explain it in purely objective terms was little short of heroic in view of the anthropomorphic babblings of the times. It was, indeed, a far cry from the notion of Romanes that the insect flies into the candle flame out of an innate curiosity to the contention of Loeb that it is forced to do so in a very literal sense when presented with the appropriate external stimulus. Among other criticisms of Loeb's theory the satirical attack of Claparède (118) is interesting. He pointed out that an observer from a distant planet might well suppose that human activity was also largely tropistic and be led to speak of the doctor-tropism, corpse-tropism, food-tropism, etc. of mankind. Somewhat later Nuel (183) made a direct application of the tropism principle to the behavior of man in a thoroughly serious but unconvincing manner (201).

From the work of Loeb, as Brett remarks, "arose a new type of comparative psychology, the mechanistic school of Bethe, von Uexküll, Th. Beer and Ziegler: for these writers the higher animals have consciousness, the lower do not." This group of physiologists were mainly interested in experimental work upon the

lower forms and insisted that physico-chemical process and the resulting behavior of the organism constituted the proper subject matter of the science within this field. They denied the validity of inferences concerning the presence and nature of mental states in lower animals, agreeing in general with Loeb that the ability to profit by experience should be the accepted criterion of psychic life, or consciousness. Moreover, they opposed the use of the subjective terminology of traditional human psychology in describing the activities of lower organisms. In a joint paper issued in 1899, Beer, Bethe, and von Uexküll (93) proposed to eliminate entirely such terms as sensation, sense-organ, memory, learning, etc. Instead of the terms hearing, smell, and sight, they would speak of phono-reception, stibo-reception and photo-reception, and for sense-organ they proposed the term reception-organ.

Loeb objected strenuously to the usual interpretation of "preference method" results in terms of sensation, choice, algedonic or aesthetic factors. He insisted that evidence for differential sensitivity was not in itself evidence of qualitatively different sensations or even of the presence of sensation at all. He believed the tropism theory could be broadened out to cover all instinctive, and perhaps even much of the socalled intelligent behavior of organisms, although he accepted consciousness as a concomitant of the higher associative processes. The theory solved, so he thought, the metaphysical problems involved in current conceptions of consciousness and volition. The importance of Loeb, in this historical connection, does not involve the question as to the ultimate truth or falsity of his special theory, either as at first announced or as later elaborated. The physico-chemical views of Verworn and Loeb provoked widespread discussion and were factors of major importance in clearing away the loose, unscientific attitude that prevailed.

Morgan, as well as Lubbock before him, maintained the right of the investigator to study the activities of animals for their own sake, without special reference to the all-absorbing controversy over mental evolution, and thus helped to give a systematic orientation to comparative psychology. Morgan's *Introduction* (176) covering the vertebrates together with Lubbock's earlier volume (167) limited largely to invertebrates were important indicators of the general trend in this direction. The canon of Morgan, which was first announced in the *Introduction* (1894) deserves to rank along with the tropism theory of Loeb as a signal attack against the current humanizing tendency. While it was distinctly less radical in spirit, nevertheless it was widely opposed at first, although it came in time to serve as the rallying cry of the more conservative group. The canon runs as follows: "In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale." This is merely the law of parsimony applied to comparative psychology; it is an insistence that the same critical attitude which had been long accepted in the methodology of general science be also adhered to in this field. Even the conservatives could hardly reject a principle so fundamental and reasonable, and the influence of this canon on the later development of the science has been most important. For though it did not rule out entirely the fallacious practice of attempting to infer the subjective life of the organism by anthropomorphic analogy, it did serve to introduce a measure of restraint into such speculation.

The influence of Morgan on the early thought of the period can hardly be overestimated. His writings show a broad sympathy and a sound scholarship in dealing with the more theoretical problems of comparative psychology that has scarcely been equalled since, except, perhaps, by Hobhouse in his *Mind in Evolution*. Nor was he a mere theorist—his contribution to early experimental developments, though somewhat limited in scope, was of first rate importance. In the *Introduction* (1894) he refers repeatedly to his genetic studies of incubated chicks and ducklings and distinguishes the types of instinctive behavior characteristic of each. In *Habit and Instinct* (1896) he gives a more complete account of this work, which he has extended, in the meantime, to include wild ducklings, moorhen chicks, and partridges. He also investigated various aspects of habit formation in young birds and emphasized the method of trial and error in animal learning. As early as 1891 (175) he speaks of the "trial and practice" element in "incomplete instincts" and of the maturation factor in "deferred instincts."

These early studies of Morgan on birds are important as marking the beginnings of the application of laboratory methods in any extensive way to the higher vertebrates. The material of *Habit and Instinct* was delivered as the Lowell Lectures in the spring of 1896 at Harvard University, and parts of it later at Chicago, New York, and other university centers, and doubtless had much to do with the outburst of experimental work in America that soon followed. Thorndike began his studies on instinct and habit formation in the chick at Harvard in the fall of 1896 and Kline independently began somewhat similar work on the chick at Clark the following year. Morgan seems to have been the first to make use of the "incubator method" in his genetic studies of birds, and his plan of keeping the young in the incubator for varying periods of time after hatching before testing them foreshadowed the more recent work of Breed and Shepard (1912).

Although the views of these four leaders regarding the nature of animal life and behavior appear to be widely divergent as individually formulated, the differences were much less important than the general points of agreement. Lubbock and Morgan, no less than Verworn and Loeb, were stoutly opposed to the older anthropomorphism. Moreover, the tropism theory of Loeb was, in a sense, merely the application of the canon of Morgan—albeit somewhat strictly—to the lower organisms. Both Lubbock and Morgan believed in adopting physico-chemical explanations of behavior in all cases in which they seemed adequate. Loeb admitted consciousness to such higher animals as gave conclusive evidence of the ability to form associations. The main point of difference concerned the stage in phylogenetic development at which the psychic factor emerged, and this is clearly a matter of minor importance in the last analysis. Furthermore, each of the leaders rejected the method of anecdote and each was a pioneer experimentalist in his own special field.

It is apparent from all the evidence at hand that a worthy beginning had been made toward the establishing of comparative psychology on a reasonably sound theoretical and experimental basis. The further development during the present century of experimental methods and results will be given in some detail in the following section. The final section will show the gradual emancipation of the subject matter of comparative psychology

from the domination of human psychology and the definite commitment of the science to an objective, natural science viewpoint.

Experimental developments

In spite of such promising beginnings, the experimental movement did not get well under way until about the opening of the present century. Aside from the experiments of Morgan on birds, only a few scattered studies had been made on the higher vertebrates. The decade centering around 1900 is especially important as marking the beginnings of laboratory work on the mammals. A more widespread application of experimental methods to lower forms also took place, as we shall see. The work began more or less independently along many lines and the leadership includes physiologists and zoologists as well as psychologists. The developments were so varied and extensive, and so much originality was shown in the application and elaboration of methods that had come down from the earlier pioneers, that this decade appears to be no less epochal than the former one had been.

Before tracing through the more important lines of progress developing out of this period, it may not be amiss to state the fundamental ground of distinction between mere observation and genuine experiment. As in all the natural sciences the distinguishing mark of experimental procedure in the strict sense is the consistent use of artificial controls resulting in precise, quantitative results. From Aristotle downward, naturalists have introduced more or less simple controls of one sort or another into field or indoor observation of behavior when an occasional problem seemed to suggest it. Usually, however, such controls have involved no more than the arrangement of a selected stimulus situation within the natural environment of the organism, without seeking to control, in any adequate way, the free movements of the animal under test. The ingenious devices of Fabre are good examples of crude attempts to control the stimulus situation in the open. The study by Galton of auditory range in birds is an interesting application of this semi-experimental method to higher forms. Galton had the quaint habit of concealing his newly invented whistle in his hands, and producing various pitches from time to time, while walking about in the zoological parks of London, in the meantime making a tabulation of the different species of bird that appeared to take note of sounds of various pitch.

In the strict sense, however, experimental behavior methods require control of both the stimulus situation and the organism under test by some appropriate technique of the laboratory type. Obviously no sharp line can be drawn between careful field observation and simple experimental procedure. In a very proper sense, the laboratory may be considered as a limited and controllable field in which isolation and quantitative measurement of selected aspects of behavior can be made. As a rule experimentalists have shown a sympathetic interest in adapting experimental situations and general living conditions in the laboratory to the natural proclivities of the animal tested, insofar as these have been adequately understood. Our emphasis upon experimental developments in this historical connection does not mean that systematic observation is to be rated as of slight value in behavior work. Field observation must always hold a place of honor in the biological sciences and particularly so in comparative psychology. Many important problems depend for their final solution upon competent field work, either wholly or in part. Nevertheless, it cannot be denied

that the development of refined experimental methods affords a good index of the growing maturity of a science, indicating an increasing ability to adequately define and solve its problems.

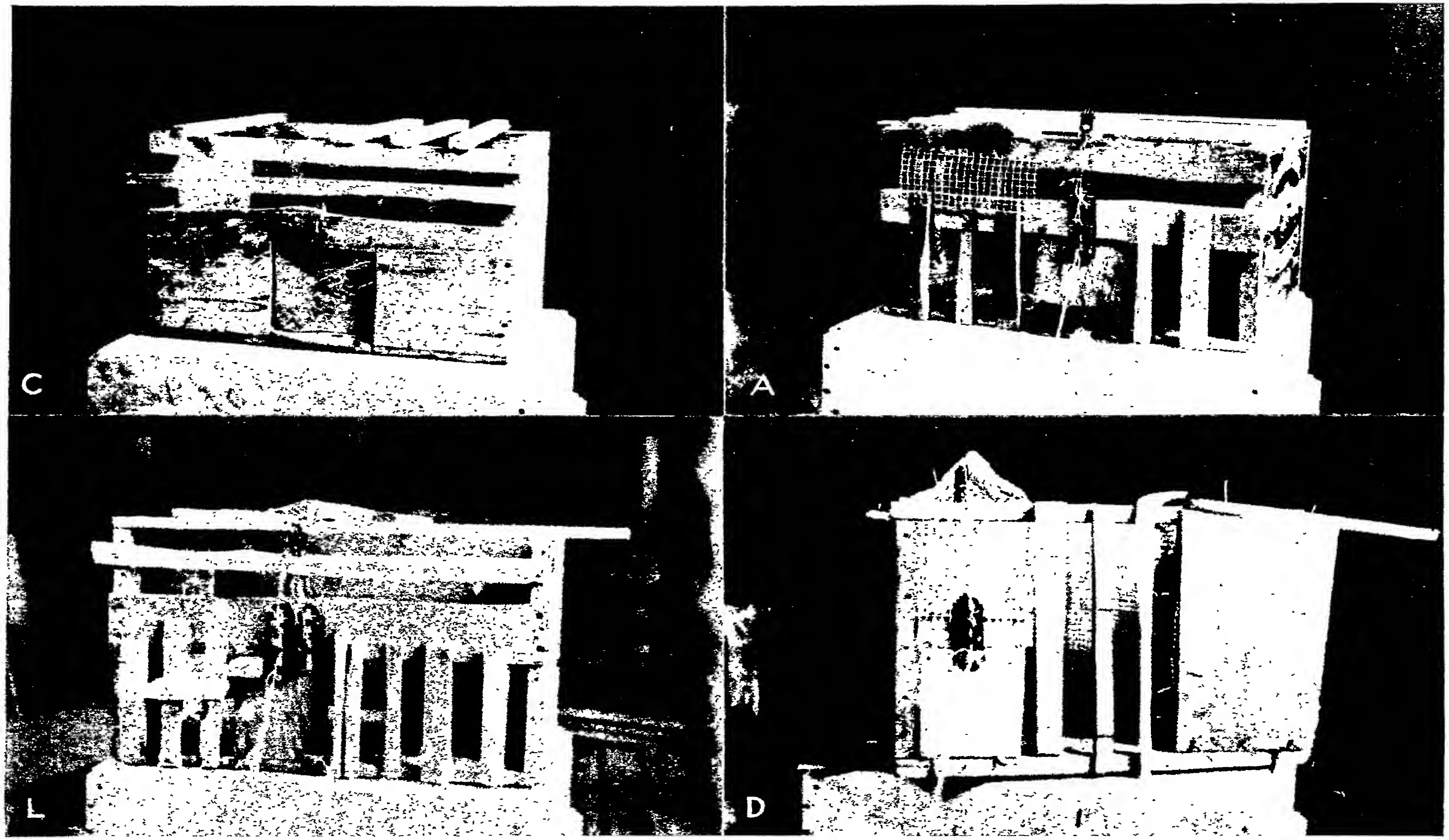
The decade centering around 1900, as stated above, witnessed a most remarkable outburst of experimental work of a highly original order in many fields. It will be convenient, in tracing out the more important lines of progress, to begin with the work on lower forms and follow systematically through to the higher. In addition to outlining the major events of the decade under review, attention will be called, from time to time, to a few of the more outstanding later developments.

The interest aroused in the sensitivity of plants by the theory and work of Darwin led to continued experimentation among the botanists (47, 53). Nemec, Haberlandt, Ricca, and later Fitting may be named among the more prominent investigators of tropistic behavior. In the field of genetics and evolution, De Vries, Bateson and others made notable contributions.

The interest in the behavior of lower organisms aroused by the work of Verworn and Loeb proved to be permanent. Loeb in particular continued to the last his experimental investigations and many of his students were inspired to enter the field and attempt to solve the problems of behavior by the physiological approach. The work of Jennings (149), which began to appear about 1897, gave a new impetus to the study of the lower organisms. Jennings—who had studied at Jena under Verworn—may be thought of as continuing the tradition of Engelmann and Verworn in contradistinction to that of Loeb. Like both of these earlier workers he was impressed by the variability of behavior even in such simple forms as the protozoa and emphasized, as Verworn had done, the internal factors in response. Jennings held that the characteristic behavior of lower forms is less simple than Loeb's tropism theory would seem to require; that their responses are typically variable to the same stimulus as their physiological states vary from time to time and from individual to individual; that instead of being direct and forced in Loeb's sense their responses are usually of the "trial and error" type, which favors modifiability. The opposing views of Loeb and Jennings may be partially explained by the fact that the former worked for the most part on sessile, or relatively inactive forms, whereas the latter studied mainly the more active, free-swimming types. As thus viewed, their work both theoretical and experimental appears to be complementary rather than antagonistic. Among other early workers on lower organisms, Parker, Holmes, Yerkes, and Mast in America; Bethe and von Uexküll in Germany, and Piéron and Bohn in France deserve special mention. Parker's study on the behavior of *Metridium* appeared in 1896, and each of the other investigators began their work on lower organisms either before, or soon after 1900.

A few scattered applications of experimental methods to the study of the behavior of the arthropoda took place during the decade. Following the rather casual test of learning ability in the crab by Bethe (1897), Yerkes adapted the maze method to this form in 1902, and extended it to the crayfish the following year. A further study of learning ability in the crab was made by Spaulding in 1904. The bulk of work on insects and other air-breathing arthropoda continued to be either field observations or semi-experimental investigations of sensory capacities and intelligence. Such careful workers as Wasmann, Forel, Claparède, and the Peckhams continuing from the

1. H. S. Jennings, 1868– ; *photograph by Science Service, Washington.* 2. G. H. Parker, 1864– *The Marshall Studio, Cambridge, Mass.* 3. E. L. Thorndike, 1874– ; *Bachrach photo.* 4. L. T. Hobhouse, 1864– ; *Elliott & Fry, London.* 5. L. W. Kline, 1866– ; *Gustav Lorey, Saratoga Springs, N.Y.* 6. W. S. Small, 1870– ; *from a photograph.*



By permission of E. L. Thorndike from original photographs supplied by R. M. Yerkes; for complete description of boxes see Animal Intelligence, pp. 31–34.

SPECIMENS OF APPARATUS DEVISED BY THORNDIKE

BOX C (15 x 20 x 12 in.). *Simple One-Act Mechanism.* Door fell inward and released animal when button, which turned on nail above door, was raised.

BOX L (15 x 20 x 12 in.). *Complex Three-Act Mechanism.* Door opened when following devices were operated in any order; loop as in Box A; left bolt drawn by clawing cord stretched across box near top; wooden bar lifted by depressing lever extending 5 in. into box.

BOX A (15 x 20 x 12 in.). *Simple One-Act Mechanism.* Door opened when bolt was drawn by clawing or biting at wire loop suspended 6 in. from floor in front center of box.

BOX D. *Imitation Test.* Imitatee in left compartment (13 x 16 x 12 in.) pulled loop (3 in. dia.) suspended 6 in. from floor, attaching above to cord running from bolt across pulleys at front and back o. box; imitator observed from right compartment (7 x 16 x 12 in.).

preceding century, and Bethe, Buttel-Reepen, and Wheeler among the later workers made worthy contributions to our knowledge of insect behavior. The work of Bethe (100, 101, 103) on the ant and bee will serve as examples of the more strictly experimental type of investigation. In 1899, Kline (154) extended the maze method to the wasp, and in 1901, Fielde employed, in her study of the ant, a maze more complex than any Lubbock had used.

The extensive work of Parker (185, 186) on fishes, which began about 1902, may be taken to mark the beginning of a more systematic study of the behavior of the lower vertebrates than had hitherto been made. The contribution of Parker and his pupils in America, and later that of Hess (142) and others in Germany, has been confined mainly to the field of sensory capacities. The earliest study of habit formation in lower vertebrates seems to have been that of Thorndike (1899) on *Fundulus*, making use of a four compartment maze. The well-known experiment of Triplett (216) on the perch appeared two years later. Aside from several early experiments on the auditory sensitivity of the frog, Yerkes deserves credit for having adapted the maze method to the turtle in 1901, and to the frog two years later.

The most important event of the decade by far was the application of laboratory methods to the higher vertebrates on an extensive scale. An excellent beginning had been made by Morgan in his simple tests of instinctive and learning capacities in the chick, and in other species of birds. Morgan's work on the chick was followed up by Thorndike (212) and by Kline (154), both of whom made use to some extent of the incubator method of Morgan. The work on learning and imitation in the chick was further extended by Thorndike, who arranged more complex problem situations than Morgan had done. His improvised labyrinths of simple design, made by setting up books, or other small objects, represent the first use of the maze method on birds. A little later Small devised the Hampton Court maze, which was used in the original or modified form by Porter, Rouse and other early workers in their systematic studies of the behavior of birds.

To Thorndike, working at Harvard and Columbia, and to Kline and Small of the Clark University laboratory belongs the credit for independently adapting experimental methods to the study of mammals. As early as 1897–98, Thorndike and Kline devised various types of problem box, the monograph (212) of the former on the cat and dog appearing in June, 1898, while the first report (154) of the latter on the white rat was published the following January. A second report by Kline appeared in April, 1899 (155), while the more complete investigation of Small making use of Kline's problem boxes was published in January, 1900. During the two years previous, Small had made a careful genetic study of the behavior of the white rat, and had constructed the well-known Hampton Court maze. In January, 1901, he reported his now classic maze-learning experiment on the white and brown rat, including also preliminary tests on the rôle of smell and vision. This was the first application of the maze method to mammals; in fact, the term "maze" and the now general use of this method in the animal laboratory dates from the work of Small. The white rat, first used in behavior work by Kline and Small, soon became the standard laboratory animal in connection with the more systematic lines of research.

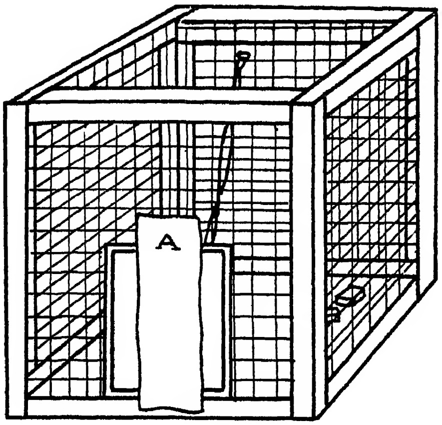
Although the credit for beginning the experimental work on mammals properly

belongs to Thorndike, Kline, and Small, the influence of previous workers, particularly Lubbock, should not be overlooked. As we have already noted Lubbock originated both problem method and maze method, and used both extensively in his study of insects. In answering the criticism of Mills against his own work, Thorndike (211) expressly states that "Lubbock used practically the same method with insects" and remarks that it is "odd" that Lubbock's principle of interposing an obstacle between an animal and some incentive such as food, etc. had not been "sooner followed with mammals." The influence of Mills is seen clearly also in Small's genetic study of the white rat. As early as 1886, Mills (171, page 31) had organized an association for the study of comparative psychology at McGill University and his later observations on both wild and domestic animals, particularly the cat, have served as a model for most later genetic studies. After making due allowance for earlier influences, it must be granted that the task of adapting these experimental methods to the mammals required a high order of originality and ingenuity. The problem situations of Thorndike and Kline were, after all, quite different from those of Lubbock, while the maze of Small was more like the wasp maze of Kline than the simple paper mazes of Lubbock.

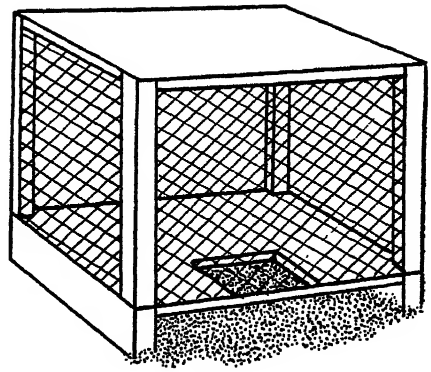
The problem boxes of Thorndike naturally differed from those of Kline, since each had planned puzzle devices with special reference to the particular type of animal to be tested. The general method of the two men differed also in one important respect. Thorndike confined his animal within the problem boxes, placing the incentive on the outside, or in certain cases utilizing mere escape from the apparatus as the incentive. Kline and Small, on the other hand, adopted the more natural method of placing the incentive within the problem box, thus leaving the animal relatively unrestrained in working the puzzle device and securing the food inside. The techniques employed in the study of imitation also differed in much the same way. Thorndike confined the imitator in a compartment immediately adjacent to the puzzle box requiring it to observe the imitatee attacking the problem through a screen or through openings in the side of the box. Kline and Small, and later Hobhouse and Porter, allowed the imitator and imitatee to work at the puzzle device together without restraint.

The main criticisms urged against Thorndike's work on the cat and dog by such men as Morgan (178, 212, review), Hobhouse (143), Kline (153) and Small (209) centered around the alleged unnaturalness of confining his animals in such small boxes (c. $20 \times 15 \times 12$ in.). Mills, with less show of judgment, went further and insisted that valid results could not be secured on the higher animals by laboratory methods. He (172, 173) criticised not only the work of Thorndike but also that of Kline, Small, and Hobhouse, all of whom had taken unusual care to make the test situation natural. Although neither Small nor Thorndike found evidence of rational imitation in common mammals, the conclusions of the latter were especially singled out for attack, largely because of the controversial style in which they were presented. It was quite generally urged also that the negative finding of a single study did not afford sufficient support to Thorndike's general denial of imitative and rational learning in all mammals below the primates.

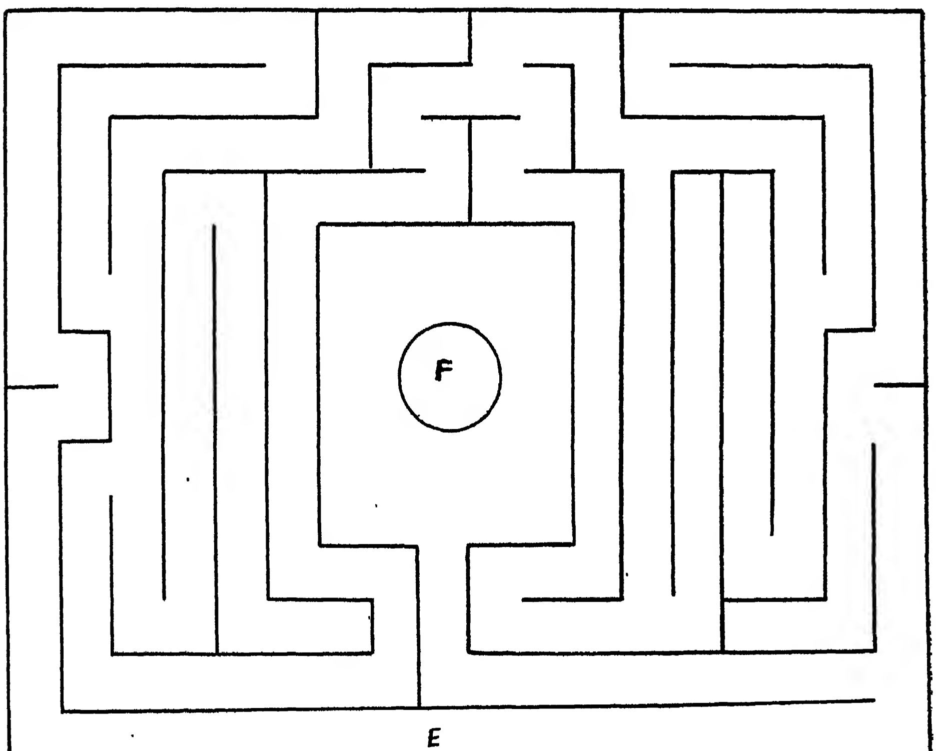
From these beginnings the laboratory study of the higher vertebrates spread



1



2



3

EARLY APPARATUS OF KLINE AND SMALL

FIG. 1. *Simple Problem Box* (7 x 7 x 6 in.). By scratching, biting or gnawing away the strip of paper, *A*, which released the door and allowed it to be pulled upward by the spring or rubber band, the box could be entered and food obtained. After Kline (154, 155).

FIG. 2. *Sawdust Box* (7 x 7 x 6 in.). By digging away the sawdust at the proper place, the box could be entered and food obtained. Both this and the box of figure 1 were placed in a large observation cage (16 x 20 x 16 in.) during experimentation. After Kline (154, 155).

FIG. 3. *Hampton Court Maze* (6 x 8 ft.). The pathways were made of wire mesh (½ in.) sides, four inches in width and depth. Entering at *E*, the animals were required to run through the labyrinth to food placed in the dish, *F*, in the center. After Small (209).

1. R. M. Yerkes, 1876– ; *from a photograph.* 2. Henri Piéron, 1881– ; *from a photograph.* 3. I. P. Pavlov, 1849– ; *photograph by Science Service, Washington.* 4. V. M. Bekhterev, 1857–1925; *from Die Medizin der Gegenwart with per. Felix Meiner, Leipzig.* 5. J. B. Watson, 1878– ; *photo by Bachrach.* 6. H. A. Carr, 1873– ; *photograph by Science Service, Washington.*

rapidly and widely. During the years 1899–1900 Thorndike (212) in America and Hobhouse (143) in England, working independently, extended experimental methods to the monkeys, the reports of both appearing in 1901. Hobhouse was interested primarily in imitative and ideational behavior and tested the cat, dog, otter, and elephant as well as the monkey and chimpanzee. Like the Clark group, he allowed his animals considerable freedom of movement when under test, and Thorndike (212, page 190) himself in his work on monkeys adopted the more natural method of placing the incentive inside and the animal outside the problem boxes. Although Hobhouse was doubtless influenced by the previous work of Thorndike, Kline and Small in America, he devised several new and ingenious tests which have proven to be of great value, especially in the study of primates. Several of these, such as the draw-in test, lock and key test, box and pole text, box placing test, and what we now call the "*Umwege*" test, have been used with minor modifications by Shepherd, Watson, Yerkes, Köhler and other later students of primate behavior.

The study of mammalian behavior was fostered in America by the psychologists and several important research laboratories were established almost immediately. The work of Thorndike did not lead to the establishment of an animal laboratory unit at Columbia. At Clark, however, regular facilities for animal research were provided as early as 1898, under the supervision of Kline, who also offered a practicum in comparative psychology. Hall, and particularly Sanford gave encouragement to the new venture. Porter's studies on birds were begun in 1901, and Kinnaman's work on monkeys, making use of the Thorndike type of problem box and the Hampton Court maze, began about the same time. The laboratory at Clark (119) represents the first attempt of American psychologists to place the new experimental science on a permanent, institutional footing.

A research laboratory was established by Watson in 1903 at the University of Chicago. During the two preceding years, Watson had been engaged at Chicago in making a genetic study of the behavior of the white rat, including a comparison of neurological maturation at the different age levels. He began with apparatus patterned after that of Kline and Small, but in the course of the work devised the inclined plane problem box for rodents as well as several new types of maze, and greatly improved the technique of Small for isolating the sensory factors in maze learning. The *Animal Education* (1903) of Watson stands out as being the most systematic and comprehensive psychobiological investigation of a mammalian form that appeared during the decade under review. An important series of researches involving operative methods was begun by Watson, assisted by Carr, in 1905 (229, 114) to determine the sensory factors involved in rodent maze learning. In 1908, Watson established a research laboratory at the Johns Hopkins University, the work at Chicago being continued under the supervision of Carr. Among other valuable contributions to methodology, Watson (259) should be credited with the color vision apparatus of the standard Yerkes-Watson discrimination method (1911) and the well known Watson circular maze. In variety, amount and importance of experimental contribution during the past quarter century, Watson ranks second to none among the psychological group.

Carr early became interested in an analysis of the problem of animal-human

learning. He (113) was the first to make use of a human maze (1911) and originated the stylus maze as a means of comparing more directly the motor learning of rodent and man. The work of Perrin, Webb, Pechstein, and Wiltbank represents the beginnings of the use of the maze in the analysis of the learning process for which the Chicago laboratory under the leadership of Carr has become so justly noted. Carr also devised the alternation problem (109) and made important contributions to our knowledge of the temporal factor in the formation of associations in animals. In 1909, Carr originated the delayed reaction method, using the white rat, and this was later extended by Hunter to the dog, raccoon, and human child.

The first important contribution of Yerkes to mammalian behavior was *The Dancing Mouse* (1907). In 1899 he established an animal laboratory at Harvard University (254) and, as we have noted, did worthy pioneer work in the application of experimental methods to the invertebrates and lower vertebrates. In connection with his study of the dancing mouse, Yerkes developed a general method of testing animal discrimination in which both reward and the electric shock as punishment could be utilized. This method was further standardized as the Yerkes-Watson discrimination method in 1911, Yerkes (259) being responsible for the animal control section and the light vision apparatus. The Yerkes Multiple Choice method (256) was devised in 1913 for the study of ideational behavior in higher vertebrates, and such forms as the crow, pig, monkey, orang-utan, chimpanzee and gorilla have been tested by this method by Yerkes, with the collaboration in some cases of his pupils. The work of Haggerty (1899) on imitation in monkeys was one of the more important early studies from the Harvard laboratory, which was very prolific under the direction of Yerkes.

A number of scattered investigations of mammalian behavior among the earlier work also deserve mention. Allen's study (1904) of the guinea-pig was somewhat similar to Watson's genetic study of the white rat which appeared the previous year. The work of Cole and of Davis on the raccoon (1907) marks the beginning of experimentation on that form. Berry tested imitation in the white rat (1906) and in the cat (1908), Yoakum (1909) made a series of laboratory tests on the squirrel, and Shepherd (1910) added his study to the work already done on the monkey. A valuable contribution to laboratory methods was made in 1911 by Hamilton (139) in originating the Quadruple Choice method, which has been extensively used by him in the analysis of reaction-types in the higher vertebrates.

At approximately the same time that Thorndike, Kline and Small began their laboratory studies on mammals in America, Pavlov, the Russian physiologist, was beginning his work on the conditioned salivary reflex of the dog. The primary interest of Pavlov and his earlier pupils was in brain physiology rather than in the behavior aspect of their work, and the broad application of the conditioned reflex, or response, method to the analysis of animal and human behavior has come more largely from the writings of Bekhterev and other psychologists. The earliest characteristic experiments in conditioning were those of Boldireff (Pavlov's Lab., 1904–5) including as secondary stimuli nearly all modalities. In 1907 Bekhterev and his pupils extended the method to the respiratory mechanism of dog and man; in 1908 to the human speech reflexes; in 1909 and later to vasomotor movements and to the motor reflexes of

finger, knee, and foot. In 1907, Krasnogorski began using the method in the analysis of infant and child behavior. About the same time the conditioned reflex method was carried to Germany by Nicolai and Kalischer and became known to the English speaking world through Pavlov's Huxley lecture (187) and later writings. The early work of Watson and Lashley (234) had much to do with creating an interest in the method in America. The method was adapted by Zeliony (Pavlov's Lab., 1905) to the investigation of sensory discrimination in animals and has been employed by the Russian school since in much the same way as the Yerkes-Watson method has been used by the American group. The early use of the method in sensory discrimination work was criticised by H. M. Johnson and other American experimentalists. In 1910 Pavlov made an appeal for a sound-proof laboratory where adequate control of the stimuli could be had; this was built shortly afterward. The contribution of Pavlov and Bekhterev and of their numerous students to the analysis of both receptor and motor behavior of mammals has come to be very generally recognized and a beginning has been made toward extending their method to the lower organisms.

The experimental work on the higher vertebrates has been developed, in the main by the psychologists, particularly in America, where comparative psychology has been increasingly recognized in both class room and laboratory. *The Journal of Animal Behavior* and the *Behavior Monograph* series were established in 1911 to take care of the growing interest in research. Both were suspended in 1917 on account of world war conditions. In 1921, *The Journal of Comparative Psychology* and the *Comparative Psychology Monograph* series were begun as a continuation of the older journal and of *Psychobiology*, two volumes of which had been published during the interim. More recently, *The Journal of Genetic Psychology* and the *Genetic Psychology Monograph* series have broadened out to include studies in animal behavior. A canvass of the field (221) in 1926 showed that systematic courses in comparative psychology were being offered in no less than thirty of the leading institutions of learning in America, while twenty or more research laboratories were in active operation. Important, but less organized research work is also being carried forward by workers in various foreign countries.

Theoretical tendencies

The newer movement under the leadership of Lubbock, Verworn, Loeb, and Morgan had aimed, on the theoretical side, at the overthrow of idle speculation in comparative psychology. The immediate effect of this reaction against the post-Darwinian anthropomorphism was, however, merely to shift the speculative interest to new problems, or to the old problems as newly formulated, and to raise the general level of theoretical discussion. For several decades, comparative psychology continued to be dominated by an introspective psychology that was striving, often with small success, to break away from philosophy. Biological and metaphysical tendencies were strangely intermixed, and the occasional attempts at logical synthesis were highly arbitrary and superficial. The speculative element was eventually thrust into the background by the growing success of the experimental movement, as outlined in the previous section, and by the rise of behaviorism.

During the two decades following 1890, the theoretical discussion centered around such related topics as (1) the point in the phylogenetic series at which consciousness

may have emerged, (2) the criterion of conscious life in the individual organism, and (3) criteria of psychic levels in infra-human organisms. The futility of speculation concerning such problems became more and more apparent, and about 1912 a movement to adopt a straightforward objective, or behavioristic viewpoint came to the fore under the leadership of Watson. Since that time, comparative psychology has been attempting to readjust itself to a strictly natural science position as the logical outcome of the Darwinian conception of psychology as a biological science. An account will now be given of the more important theoretical tendencies that led ultimately to the liberation of infra-human psychology from the dominating influence of human psychology and speculative philosophy.

The tropism theory of Loeb offered a distinct challenge to the old school that had taken more or less for granted the supposition that even the lowest organisms possessed some form of psychic life. Loeb held the elemental component of all psychic life to be "the activity of the associative memory" and maintained that unless an organism could be shown to possess the capacity to form associations its behavior must be considered unconscious. "Our criterion," he says, "puts an end to the metaphysical ideas that all matter, and hence the whole animal world possesses consciousness." The logical conclusion is that tropistic and instinctive behavior is wholly unconscious and that such organisms as are incapable of definitely profiting by experience are nothing more nor less than reflex machines. This general point of view was accepted by Beer, Bethe, and von Uexküll (93), Nuel (183), Ziegler (20, 261) and others, and by Bohn (105, 107) in a somewhat modified form. On the basis of this criterion, this group contended that most probably the invertebrates generally were devoid of consciousness. At any rate, an adequate account of their behavior could be given in physico-chemical and behavior terms and without reference to any possible psychic life. In much the same vein, Titchener (215) denied consciousness to plants, although accepting the current view that all animal forms are conscious in some sense.

Bethe's contention that ants, bees and other insects are mere reflex machines stirred up no little controversy among the entomologists. Wasmann (225, 226), although denying rational intelligence to even the higher vertebrates, insisted on assigning some sort of psychic life to insects, while Buttel-Reepen (108), and especially Forel (131), held that insects give evidence of a relatively complex mental life. Forel went so far as to maintain that their behavior involves memory, associations of sensory images, perceptions, attention, habit formation, and simple powers of inference from analogy.

The attempt of Loeb and other mechanists to restrict consciousness to the higher animals on the basis of ability to form associations was brought to naught by experimental results indicating that many, if not all, of the lower organisms have such capacity to some degree. The early work of Jennings, Piéron, Yerkes and others had clearly shown this fact. Furthermore, many writers, including Romanes, Lubbock and Morgan, had pointed out the logical fallacy of denying consciousness to organisms that do not meet an arbitrary criterion of this sort.

The basic assumption of Loeb, that tropistic, instinctive, and unlearned responses in general are wholly unconscious, and hence that consciousness is coextensive with acquired, or intelligent behavior, was called in question on all

sides. Both contemporary and later psychologists and biologists usually assign some sort of awareness to the more complex instincts, even though denying the presence of a conscious, guiding purpose. Romanes, for example, defines instinct as "reflex action into which there has been imported the element of consciousness." The ability to profit by experience was to him positive evidence of consciousness in the sense of a guiding factor. Morgan held much the same view. The ability to profit by experience was maintained by him to be the criterion of effective consciousness, but he argued that for all we know, even the growth changes taking place "in the duly fertilized egg" may involve sentience, or a dim awareness. It is clear, then, that Loeb had done nothing more than take over the criterion of Romanes and make a fallacious application of it by denying consciousness outright where positive evidence of a conscious guiding factor was not forthcoming. In any case, ability to learn ceased to be of value as a criterion of consciousness as soon as modifiability of behavior in the protista had been definitely demonstrated.

The search for other criteria of consciousness, and of different psychic levels in infra-human forms proved to be hardly more successful. No one seemed to appreciate the seriousness of the difficulties involved. The fact that the introspectively derived levels of human mental life were arbitrary and based upon philosophical prejudices insofar as they were clearly defined at all was generally overlooked. Lubbock, indeed, had urged that the chief obstacle to the use of anthropomorphic analogy lay in the almost utter lack of definite correlations between mental states and bodily behavior factors in the human field. However, occasional criticisms of such a fundamental sort were ineffectual. The application of the canon of Morgan presupposes a fairly definite hierarchy of human mental processes and the possibility of recognizing corresponding levels in animals. This canon was held by many to place an undue restriction upon subjective interpretation and nothing would establish it so securely as to work out a hierarchy of mental levels that would make it a workable instrument. It is not surprising, therefore, that interest gradually shifted from the problem of determining a criterion of consciousness in animals to speculations concerning criteria of infra-human psychic levels.

Morgan himself posited three mental levels as follows: (1) sentience, a dim awareness or vague feeling state, probably possessed by all organisms, (2) effective consciousness, indicated by the ability to profit by experience which supposedly involves conscious guidance, and (3) self-consciousness, associated with highly analytical or rational processes, such as presuppose genuine language ability and therefore probably limited to man. Since he grants that all organisms are probably sentient, and insists that man alone is self-conscious in his sense, the task reduces to that of deciding what organisms meet the test of the second level. And here a structural criterion is brought in also, since Morgan seems to feel that this level requires a central nervous system and brain of some complexity (179). However, it is obvious that the distinction between the first and second level, like the criterion of Loeb, becomes meaningless insofar as evidence is forthcoming that the ability to profit by experience is common to all organisms.

Several other attempts were made to arrange hierarchies of psychic development for use in comparative psychology. Hachet-Souplet (136) proposed a classification based upon the training methods (*méthode de dressage*) to which an animal

may be responsive. The protozoa show only the psychic attribute of excitability and cannot be trained at all; certain other animals ranging from Coelenterates to mammalian forms possess primitive instincts and functional memory and are subject to coercive training; a few of the higher animals possess genuine memory and intelligence and are amenable to persuasion. Schneider (205) held the view that consciousness exhibits itself in six progressive stages as follows, the first three stages only being applicable to infrahuman organisms: ether, material, sense-quality, form, potency, and will. Kirkpatrick (151) proposed "organosis" as a common term covering both the neural and psychic factors, and recognizes four progressive types of organosis—vegetative, sensory-motor, representative and abstract thinking. Lukas (168) suggested that the criteria of consciousness be grouped under three general heads as follows, (1) morphological, including structural aspects of brain and sense-organs, (2) physiological, with emphasis upon evidences of individual purposiveness and the ideomotor factor in behavior, (3) teleological, covering the significance of various stimuli for the organism. Finally Yerkes (252) has analyzed mental activity into three levels—discriminative, intelligent, and rational—corresponding roughly to those of Morgan. He does not, like Morgan, limit the highest level to man, but agrees with Morgan that the lowest level is probably common to all animal forms.

The most systematic set of criteria offered as a basis for determining the psychic level of organisms was the following, devised by Yerkes (252):

I. Structural criteria

1. General form of organism (Organization)
2. Nervous system (Neural-organization)
3. Specialization in the nervous system (Neural-

II. Functional criteria

1. General form of reaction (Discrimination)
2. Modifiability of reaction (Docility)
3. Variableness of reaction (Initiative)

The above criteria are given in the general order of increasing importance, as diagnostic signs of psychic life, functional signs being of more importance than structural, and the particular sign within each group of more value than the general, although as Yerkes admits, this may not hold in every instance. In illustrating the application of the criteria, Yerkes examines the evidence for the sea-anemone and concludes that it shows no certain signs of either intelligent or rational consciousness, and probably possesses a psychic life on the lowest level, the discriminative. He questions whether it is not reasonable to suppose, on the basis of such criteria, that the ant "possesses a form of consciousness which is comparable in complexity of aspect and change with the human." Curiously enough, many years before Lubbock (166) had stated the case for the ant in much the same language without a definite set of criteria to guide him.

No one appeared to question the relevancy and usefulness of the concept of psychic levels as thus employed in comparative psychology. The point was quite generally overlooked that little or nothing would be gained by the mere classification of organisms into two or three rough groups of the types suggested, even if the validity of the criteria employed were granted. The subjectivists did not seem to realize that their first and foremost problem was to make an analysis of the animal consciousness, by the method of analogy, along the lines of human introspective psychology. Nor did it seem to occur to them that, to be at all adequate, such an analysis must reveal to us in terms of our own experi-

or the other animal in various typical situations. Naturally this would mean a comparison of the qualitative aspects of characteristic elementary and complex mental states of animal and man. The arrangement of organisms into a psycho-phylogenetic tree on the basis of their general psychic level should follow rather than precede a thoroughgoing analysis of their actual inner conscious experience. The principle of psychic levels as commonly employed was, in reality, only a substitute for such an analysis of experience, although often pretending to represent genuine psychological analysis.

Even those who contended that the primary purpose of comparative psychology was to secure a picture of the subjective life of infra-human forms were exceedingly cautious about hazarding an opinion regarding the qualitative aspects of animal consciousness. After spending a lifetime in the study of insects, Lubbock hesitates to do more than make a few shrewd guesses concerning their general mental level. He lays down the principle that we can know nothing whatsoever concerning the experience of animals, *qua* experience. Morgan, Wundt, Titchener, and most other later writers agree with him that even the quality of a simple sensation or feeling cannot be translated into terms of human consciousness, and hence must remain forever shrouded in mystery. But this is precisely the first and fundamental task of a subjective comparative psychology. How, indeed, can anthropomorphic analogy be successfully employed in revealing the more complex mental life of animals, if inferences regarding the qualitative aspects of the simplest mental states are admittedly impossible?

The opinion of Lubbock that the protozoan possesses most probably a vague, confused consciousness, and that of Morgan and Thorndike that the mental life of the higher vertebrates is unanalytical and devoid of free ideas, represent, even if true, logical deduction rather than psychological analysis. Among the few attempts to portray the actual feelings of the animal in human terms, that of Thorndike (212, page 123) will serve as a fair example. He compares the characteristic consciousness of the cat or dog to that of the human being while in swimming, when "one feels sense-impressions, has impulses, feels the movements he makes; that is all." Morgan "cordially endorses" this interpretation, although Thorndike is careful to say that it may be only a fancy.

It was inevitable, although extremely unfortunate, that the speculative spirit should have held so dominant a place in the earlier decades of the period, hindering as it did the normal progress of comparative psychology along naturalistic lines. The real difficulty lay in the fact that the Cartesian conception of mind as an entity was widely prevalent. This carried with it the idea that at some point in the phylogenetic scale the psychic factor as something *sui generis* had made its appearance. The whole matter had been disposed of by Descartes by sweeping aside with a grand gesture the notion of conscious life in all organisms below man. In denying consciousness to lower organisms only, Loeb, Bethe, and other extreme mechanists were faced with the problem of the origin and appearance of consciousness, and the mode of its operation in the higher animals. The view of Morgan and the later conservatives that life and mind in some sense are probably coextensive avoided the question as to the first appearance of consciousness, but substituted the equally ubiquitous one concerning the psychical level of various organisms. As we have seen, no one had

brought forward criteria of consciousness, or of psychical levels that were either logically satisfactory or of any genuine value in the practical task of arranging organisms in a mental scale. More important still, no one had made a serious attempt to reveal the subjective experience of the animal mind in terms of the analytical concepts of human consciousness.

In view of the evident failure of the defenders of subjectivism in comparative psychology to offer a constructive working program, it does not seem strange that the validity and usefulness of anthropomorphic analogy began to be attacked. The vigorous and rapid extension of experimental methods that marked the turn of the century had the effect of shifting the emphasis from speculation to objective results. The experimentalists became more and more interested in observing and reporting behavior and had less time and inclination than formerly to indulge in subjective speculation. They were, indeed, often embarrassed by the claim that their work was not genuinely psychological insofar as they failed to make a deliberate subjective interpretation of their results. When the experimentalist did stop to theorize, he was likely to do so in a more critical vein than formerly. For example, Thorndike, on the basis of his own studies, vigorously attacked imitational and ideational types of learning in higher vertebrates and emphasized, even more than Morgan had done, the trial and error factor.

Even in the field of human psychology, the older subjective concepts and the introspective method were beginning to be challenged. In 1904, James (148) led out with his famous attack on the concept of consciousness as an entity, and Cattell (116) asserted the right of the psychologist to deal with purely objective phases of human behavior without recourse to introspective or other subjective interpretation. Somewhat earlier than this, Woodworth (246) had shown the inadequacy of introspective analysis in connection with his study of voluntary movement. A decade later, Dunlap (124, 125) emphasized the shortcomings of introspection and argued against the current conception of the mental image. In philosophy, the American wing of the pragmatic movement, and more particularly the development of American realism (244, 245), had led to a demand for a reformulation of psychological conceptions, more in line with a functional, or relational view of mind. In Russia, Bekhterev (94) was contending for a strictly objective human psychology although not denying the existence of mental states paralleling behavior, stressing rather the irrelevancy of subjective description. In spite of such occasional evidences of revolt, however, human psychology was still dominated by subjectivism, as a survey of the opinions of representative leaders will show (126, 222).

Thus matters stood, when Watson, beginning about 1912, proposed that psychology throw overboard the introspective method and all subjective concepts and limit its activities to the study of objective factors in terms of stimulus-response relationships. Watson denied that the psychologist, as scientist, had any right to recognize such philosophical distinctions as mind-body, subjective-objective, conscious-unconscious. To the empirical observer there exists only the organism as an object and its movements or behavior in an environment. Such subjective categories as sensation, emotion, image, etc., as currently conceived, are logical artefacts rather than psychological entities or processes. Nothing of the sort can be discovered by natural

science methods. Such terms are meaningless to the scientist, therefore, however valuable they may be to the philosopher. The living organism presents no mind-body dichotomy to the biological observer but is, for him, a unitary object in the same sense that a crystal or other inorganic body is such for the physical scientist. Speculative analysis and interpretation, insofar as they are justified at all, belong to the philosopher; the psychologist must use a descriptive terminology that properly belongs to the scientific universe of discourse. He cannot juggle into his system subjective categories about which natural science in the nature of the case can know nothing.

We are not here directly concerned with the specific application of the objective view of Watson to human psychology. However, it may be remarked that insofar as the proper use of anthropomorphic analogy is dependent upon a well-grounded analysis of human consciousness, the behavioristic issue in human psychology is of vital importance to infra-human psychology. Moreover, the distinction at this point is not, strictly speaking, between animal and man but between that part of human psychology in which introspection is possible and the remainder of the field, both animal and human. As Morgan (176) early pointed out, the mental life of the human infant, and certain types of the subnormal and insane can be approached only by the method of analogy applied precisely as in the animal field. From the organismic principle underlying the behavioristic position it would follow that only such data on the normal adult human as can be obtained by objective methods properly belong in a comparative psychology broad enough to include the human species. The view of Watson and of other leading behaviorists (159, 238) is that the entire range of human experience may be formulated in objective terms and exhaustively investigated when appropriate natural science methods have been developed.

The success of the objective movement in the infra-human field meant the overthrow of the principle of anthropomorphic analogy. The special dangers involved in the method of analogy had been emphasized by Lubbock, Morgan, Wundt, and many other writers who, in general, defended its use. In his earliest phase, Verworn had stated the obvious logical principle that the greater the similarity between an organism and man the greater the validity of inferences regarding the psychic life of the former. He appears to have been the first to make use of the now familiar formula: $X:A::C:B$, in which the first two terms represent the infra-human and human mental states respectively, and the last two terms the corresponding bodily and behavior characteristics. In criticising Verworn's formula, Norman (182) has shown how utterly unreliable it may be when applied to specific cases. The logical implications of the method of analogy were most lucidly and comprehensively treated by Morgan in the first chapter of his *Introduction*, in which he also lays down the canon which bears his name. Morgan here stresses the fact that a subjective human psychology is dependent upon ego-centric analogy in much the same way as a subjective animal psychology is dependent upon anthropomorphic analogy, and offers the only escape from the predicament of solipsism. The behaviorists accepted the reasoning of Morgan, but rejected both types of analogy as being not only fallacious but unnecessary. The leading subjectivists were agreed that analogy, unless applied with extreme caution, was likely to be dangerously speculative, whereas Watson

and the behaviorists went the logical limit by holding that the speculative element was so large as to render all inferences of this sort misleading, and scientifically worthless.

The objective principle as applying to the infra-human field, has come to be more and more accepted, and at present, represents the dominant tendency in comparative psychology. Although the validity of analogy is insisted upon by some writers (252, 223) they make little or no use of it. It is generally agreed that the qualitative aspects of the animal consciousness cannot be inferred from structure or behavior. But this, as we have seen, is tantamount to giving up the primary task of the subjective method and carries with it the implication that a subjective comparative psychology is quite impossible. In view of the strength and vigor of the objective movement, it seems fair to conclude that the science has definitely adopted a strictly biological viewpoint and a natural science methodology. Its major categories—organism, environment, and response, or behavior—are broadly naturalistic, and avoid the older mind-body dichotomy with its attendant speculations. The proper goal of this objective comparative psychology is the determination of the conditions and laws of stimulation-response process, involved in the continuous interaction between the organism and its environment.

Having freed itself from the dominating influence of human psychology insofar as subjective interpretation is concerned, comparative psychology no longer need be bound by the older anthropocentric attitude as to its legitimate purposes and program. Indeed, it gives some promise of discarding the narrow view that it exists as a mere adjunct to human psychology and that its primary aim should be to make discoveries that may throw light upon the mental processes or behavior of the human species. Even so conservative a writer as Wundt (247) recognized the right of comparative psychology to develop a content independent of human reference in the same sense as zoology is independent of human morphology and physiology. This broader view would seek to find intrinsic interest in the behavior of each organism studied, including man, and in all possible intercomparisons of such behavior. The differences in behavior between ameba and earthworm may very well be of more interest and importance in the systematic development of the science than behavior differences between chimpanzee and man. Just as morphology and physiology in their comparative aspect include the entire range of structural and functional differentiation in living organisms, so comparative psychology should seek to study the multitudinous modes of adjustment of these same organisms to their larger environment.

LIST OF LITERATURE

GENERAL

(1) Aristotle. 1910–12. The Works of Aristotle translated into English. Oxford, Clarendon Press. (Historia Animalium, Vol. 4, 484p.; minor biological treatises, Vol. 5, 552 p.)

(2) Brett, G. S. 1912–21. A History of Psychology. London, Allen, 3v.

(3) Carus, J. V. 1872. Geschichte der Zoologie bis auf Joh. Müller und Charles Darwin. München, Oldenbourg, 738p. Fr. Tr. Hogenmüller, 1880. Paris, Ballière, 623p.

(4) Cuvier, G. 1841–45. Histoire des sciences naturelles depuis leur origine jusqu'à nos jours. Paris, Fortin, 5v. in 4.

(5) Descartes, R. 1911–12. The Philosophical Works. Eng. Tr. Haldane and Ross. Cambridge, Univ. Press, 2v.

(6) FOSTER, M. 1901. Lectures on the History of Physiology during the Sixteenth, Seventeenth and Eighteenth Centuries. Cambridge, Univ. Press, 310p.
(7) HAMMOND, W. A. 1902. Aristotle's Psychology. A Treatise on the Principle of Life. (De Anima and Parva Naturalia.) London, Sonnenschein, 339p.
(8) HASKINS, C. H. 1924. Studies in the History of Mediaeval Science. Cambridge, Univ. Press, 411p.
(9) LEWES, G. H. 1864. Aristotle: A Chapter from the History of Science. London, Smith, 404p.
(10) LOCY, W. A. 1915. Biology and its Makers. 3rd Rev. Ed. New York, Holt, 469p.
(11) ———. 1925. The Growth of Biology. New York, Holt, 481p.
(12) MIALL, L. C. 1912. The Early Naturalists: Their Lives and Work (1530–1789). London, Macmillan, 396p.
(13) RADL, E. 1909–13. Geschichte der biologischen Theorien in der Neuzeit. 2. gänzlich umbearb. Aufl. Leipzig, Engelmann, 2v.
(14) SINGER, C. J. 1922. Greek Biology and Greek Medicine. Oxford, Clarendon Press, 128p.
(15) ———. (Editor) 1917–21. Studies in the History and Method of Science. Oxford, Clarendon Press, 2v.
(16) THOMSON, J. A. 1899. The Science of Life: an Outline of the History of Biology and its Recent Advances. New York, Stone, 246p.
(17) THORNDIKE, E. L. 1923. A History of Magic and Experimental Science during the First Thirteen Centuries of our Era. New York, Macmillan, 2v. (See also Natural science in the middle ages. Pop. Sci. Mon. 1915. 87:271–91).
(18) WARDEN, C. J. 1927. A Short Outline of Comparative Psychology. New York, Norton, 96p.
(19) WILM, E. C. 1925. The Theories of Instinct: a Study in the History of Psychology. New Haven, Yale Univ. Press, 188p.
(20) ZIEGLER, H. E. 1910. Der Begriff des Instinktes einst und jetzt: eine Studie über die Geschichte und die Grundlagen der Tierpsychologie. 3rd Ed. 1920. Jena, Fischer, 112p.

THE ANECDOTAL PERIOD

(21) ANGELL, J. R. 1909. The influence of Darwin on psychology. Psychol. Rev., 16:152–69. (See pages 143–218 for complete symposium on influence of Darwin on mental and moral science and philosophy).
(22) BATES, H. W. 1863. The Naturalist on the River Amazons. 3rd Ed. 1873. London, Murray, 394p.
(23) BELT, T. 1874. The Naturalist in Nicaragua; with Observations on Animals and Plants in Reference to the Theory of the Evolution of Living Things. London, Murray, 403p.
(24) BINET, A. 1888. La vie psychique des micro-organismes. Paris, Doin, 307p. Eng. Tr. McCormack, 1889. Chicago, Open Court, 120p.
(25) BREHM, A. E. 1864. Tierleben: allgemeine Kunde des Tierreichs. 4th Ed. 1911–22. Ed. by zur Strassen. Leipzig, Bibliogr. Institut, 13v.
(26) BÜCHNER, L. 1876. Aus dem Geistesleben der Tiere, Leipzig, Thomas, 408p. Eng. Tr. Mind in Animals, from 3rd Rev. Ed. Besant, 1903. London, Bonner, 359p.
(27) CARTER, M. H. 1897. Darwin's idea of mental development. Amer. J. Psychol., 9:534–59.
(28) ———. 1899. Romanes' idea of mental development. Amer. J. Psychol., 11:101–18.
(29) DARWIN, C. R. 1859. The Origin of Species. 6th Ed. 1872. New York, Appleton, 2v. in 1. (See appendix Romanes' Mental Evolution in Animals for posthumous essay on instinct. Originally written for this volume.)
(30) ———. 1871. The Descent of Man. New York, Appleton, 2v.
(31) ———. 1872. The Expression of the Emotions in Man and Animals. New York, Appleton, 372p.
(32) ———. 1875. 2nd Ed. The Movements and Habits of Climbing Plants. London, Murray, 208 p.
(33) ——— . 1875. Insectivorous Plants. London, Murray, 462p.
(34) ———. 1877. Biographical sketch of an infant. Mind, 2:285–94.
(35) ———. 1880. (with F. Darwin). The Power of Movement in Plants. New York, Appleton, 592p.
(36) ———. 1881. The Formation of Vegetable Mould through the Action of Worms; with Observations on their Habits. London, Murray, 326p.
(37) DARWIN, F. 1887. Life and Letters of Charles Darwin. London, Murray, 3v.
(38) DU CHAILLU, P. B. 1861. Explorations and

Adventures in Equatorial Africa. London, Murray, 479p.

(39) Espinas, A. 1877. Des sociétés animales. 3rd Ed. 1924. Paris, Alcan, 454p.

(40) Fabre, A. 1910. The Life of J. H. Fabre, the Entomologist. Eng. Tr. Miall. London, Hodder, 299p. (See biog. note by Wheeler. 1916. J. Anim. Behav., 6:74–80).

(41) Fabre, J. H. 1879–1907. Souvenirs entomologiques. Paris, Delagrave, 10v.

(42) ———. 1913. Les merveilles de l'instinct chez les insectes. Paris, Delagrave, 271p. Eng. Tr. The Wonders of Instinct: Chapters in the Psychology of Insects. Teixiera de Mattos and Miall, 1918. London, Unwin, 320p.

(43) ———. 1913. Social Life in the Insect World. New York, Century, 327p.

(44) Fechner, G. T. 1848. Nanna oder über das Seelenleben der Pflanzen. 2nd Ed. 1899. Leipzig, Bosz, 300p.

(45) Fiske, J. 1875. Outlines of Cosmic Philosophy. New Ed. 1903. Boston, Houghton-Mifflin, 4v.

(46) Geddes, P. 1886. A synthetic outline of the history of biology. Proc. Roy. Soc. Edinburg, 13:904–10.

(47) Green, J. R. 1909. A History of Botany (1860–1900). Oxford, Clarendon Press, 543 p. Chap. 10, 11.

(48) Haeckel, E. 1874. Anthropogenie oder Entwickelungsgeschichte des Menschen (Historischer Theil, S. 1–92). Leipzig, Engelmann, 732p.

(49) ———. 1882. Die Naturanschauung von Darwin, Goethe und Lamarck. Jena, Fischer, 64p.

(50) ———. 1887. Zellseelen und Seelenzellen. New Ed. 1907. Leipzig, Kroner, 51p.

(51) ———. 1899. Die Welträtsel. Bonn, Strauss 473p. Eng. Tr. McCabe, 1901. New York and London, Harper, 390p.

(52) Hartmann, R. 1885. Anthropoid Apes. London, K. Paul, 326p.

(53) Harvey-Gibson, R. J. 1919. Outlines of the History of Botany. London, Black, 274p. Chap. 7, 10 and 11.

(54) Houzeau, J. C. 1872. Études sur les facultés mentales des animaux comparées à celles de l'homme, par un voyageur naturaliste. Mons, Manceaux, 2v.

(55) Howard, D. T. 1927. The influence of evolutionary doctrine on psychology. Psychol. Rev., 34:305–12.

(56) Hudson, W. H. 1892. The Naturalist in La Plata. 6th Ed. 1922. New York, Dutton, 394p.

(57) Huxley, T. H. 1863. Evidence as to Man's Place in Nature. New York, Appleton, 184p.

(58) ———. 1874. On the hypothesis that animals are automata, and its history (Belfast address). Also other essays on methods and results. Collected Essays, v.1. New York, Appleton, 430p.

(59) ———. 1893. Evolution and Ethics (Romanes lecture). London and New York, Macmillan, 57p.

(60) ———. 1893. Darwiniana. Collected Essays, v. 2. New York, Appleton, 475p.

(61) ———. 1921. Charles Darwin. London, Watts, 119p. (See also recent biographies of Darwin by Bradford, Dorsey, and Ward).

(62) Kussmaul, A. 1884. Untersuchungen über das Seelenleben des neugeborenen Menschen. Tübingen, Moser, 32p.

(63) Lamarck, J. B. 1809. Philosophie zoologique. Paris, Dentu, 2v. Eng. Tr. Elliot, 1914. London, Macmillan, 410p.

(64) Lankester, E. R. 1892. The History and Scope of Zoology. New York, Humboldt, 58p. (See also article *Zoology* Encyc. Brit.)

(65) Leroy, C. G. 1781. Lettres philosophiques sur les animaux. The Intelligence and Perfectibility of Animals. Eng. Ed. 1870. London, Chapman and Hall, 272p.

(66) Lindsay, W. L. 1879. Mind in the Lower Animals. (Bibliography of 133 titles). London, K. Paul, 2v.

(67) Marey, E. J. 1873. La machine animale: locomotion terrestre et aérienne. Paris, Ballière, 299p. Eng. Tr. 1874. New York, Appleton, 283p.

(68) Osborn, H. F. 1894. From the Greeks to Darwin. New York, Scribners, 259p.

(69) Peckham, G. W. and E. G. 1881–93. Miscellaneous Works. Ten pamphlets in 1v.

(70) Perty, M. 1876. 2nd Ed. Über das Seelenleben der Tiere. Leipzig, Winter, 719p.

(71) Poulton, E. B. 1890. The Colors of Animals: their Meaning and Use. New York, Appleton, 360p.

(72) Preyer, W. 1881. Die Seele des Kindes. 5 Aufl. 1900. Leipzig, Grieben, 448p. Eng. Tr. Brown, 1888–89. New York, Appleton, 2v.

(73) ———. 1886. Über die Bewegungen der Seesterne. Mitt. zool. Stat. Neapel., 7:27–128; 191–233.

(74) Romanes. G. J. 1881. Animal Intelligence. London, K. Paul, 520p.
(75) ———. 1883. Mental Evolution in Animals. London, K. Paul, 411p.
(76) ———. 1885. Jelly-fish, Starfish and Sea-urchins. New York, Appleton, 323p.
(77) ———. 1888. Mental Evolution in Man. London, K. Paul, 452p.
(78) ———. 1892–7. Darwin, and after Darwin. Chicago, Open Court, 3v.
(79) ———. 1897. Essays. Ed. by C. L. Morgan. New York, Longmans, 253p.
(80) Schneider, G. H. 1880. Der thierische Wille. Leipzig, Abel, 447p.
(81) ———. 1882. Der menschliche Wille von Standpunkte der neueren Entwickelungs-theorien. Berlin, Dümmler, 498p.
(82) Semper, K. 1881. Animal Life as affected by the Natural Conditions of Existence. New York, Appleton, 472p.
(83) Spalding, D. A. 1873. Instinct, with original observations on young animals. Macmillan's Mag., 27:283–93. (Reprinted 1902. Pop. Sci. Mon., 61:126–42).
(84) ———. 1875. Instinct and acquisition. Nature, 12:507–8.
(85) Spencer, H. 1855. Principles of Psychology. 3rd Ed. 1894. New York, Appleton 2v.
(86) ———. 1864–7. Principles of Biology. Popular uniform ed. 1910–15. New York, Appleton, 2v.
(87) Wallace, A. R. 1869. The Malay Archipelago. 17th Ed. 1922. New York and London, Macmillan, 515p.
(88) ———. 1889. Darwinism. London, Macmillan, 494p.
(89) Wasmann, E. 1906. Die moderne Biologie und die Entwicklungstheorie. Freiburg, Herder, 529p. Eng. Tr. from 3rd Ed. Buchanan, 1923. St. Louis, Herder, 539p.

THE EXPERIMENTAL PERIOD

(90) Allen, J. 1904. The associative processes of the guinea pig. J. Comp. Neurol., 14:293–359.
(91) Angell, J. R. 1913. Behavior as a category of psychology. Psychol. Rev., 20:255–70.
(92) Baldwin, J. M. 1905. Sketch of the history of psychology. Psychol. Rev., 12:144–65.
(93) Beer, T., Bethe, A., und Uexküll, J. v. 1899. Vorschläge zu einer objectivirenden Nomenclatur in der Physiologie des Nervensystems. Biol. Zbl., 19:517–21.
(94) Bekhterev, V. M. 1913. Objective Psychologie. Leipzig, Teubner, 468p. Fr. Tr. Kostyleff, 1913. Paris, Alcan, 478p. (Note: first appeared in Rus. 1907).
(95) ———. 1913. Sur le psychoreflexologie ou psychologie objective. Arch. int. Neurol., 1:273–88; 365–74.
(96) ———. 1923. Die Medizin der Gegenwart in Selbstdarstellungen. (Autobiographical sketch with author's list of 118 references) 6:52p.
(97) ———. 1926. Allgemeine Grundlagen der Reflexologie des Menschen. Leipzig, Wein, Deuticke, 436p. Tr. from 3rd Rus. Ed. 1923.
(98) Berry, C. S. 1906. The imitative tendency of white rats. J. Comp. Neurol., 16:333–61.
(99) ———. 1908. An experimental study of imitation in cats. J. Comp. Neurol., 18:1–25.
(100) Bethe, A. 1898. Dürfen wir den Ameisen und Bienen psychische Qualitäten zuschreiben? Pflügers Arch., 70:15–100.
(101) ———. 1898. Das Centralnervensystem von *Carcinus maenas*, II. Arch. mikr. Anat., 51:382–452.
(102) ———. 1900. Noch einmal über die psychischen Qualitäten der Ameisen. Pflügers Arch., 79:39–52.
(103) ———. 1902. Die Heimkehrfähigkeit der Ameisen und Bienen. Biol. Zbl., 22:193–238.
(104) Bohn, G. 1904. Les premières lueurs de l'intelligence. Bull. Inst. gen. psychol., 4:419–35.
(105) ———. 1905. Les tropismes, les reflexes, et l'intelligence. Année psychol., 12:137–56.
(106) ———. 1909. La naissance de l'intelligence. Paris, Flammarion, 350p. (See rev. by Jennings. 1909. Amer. Natur., 43:619–33).
(107) ———. 1911. La nouvelle psychologie animale. Paris, Alcan, 200p. (See rev. by Yerkes. 1906. J. Comp. Neurol., 16:231–8).
(108) Buttel-Reepen, H. v. 1900. Sind die Bienen Reflexmaschinen? Biol. Zbl., 20:97–109; 130–44; 177–93; 209–24; 289–304. Eng. Tr. Geisler, 1907. Medina, Root, 48p.
(109) Carr, H. A. 1917. The alternation problem. J. Anim. Behav., 7:365–84.
(110) ———. 1917. Maze studies with the white rat. J. Anim. Behav., 7:259–75; 277–94; 295–306.

(111) Carr, H. A. 1919. Length of time interval in successive association. Psychol. Rev., 26: 335–53.

(112) Carr, H. A. (with Freeman, A. S.) 1919. Time relationships in the formation of associations. Psychol. Rev., 26:465–73.

(113) Carr, H. A. (with Hicks, V. C.) 1912. Human reactions in a maze. J. Anim. Behav., 2:98–125.

(114) Carr, H. A. and Watson, J. B. 1908. Orientation in the white rat. J. Comp. Neurol., 18:27–44.

(115) Cason, H. 1925. The conditioned reflex or conditioned response as a common activity of living organisms. Psychol. Bull., 22:445–72.

(116) Cattell, J. M. 1904. Conceptions and methods of psychology. Pop. Sci. Mon., 66:176–86.

(117) Claparède, É. 1901. Les animaux sont-ils conscients? Rev. philos. France Étrang., 51: 481–98. Eng. Tr. Davis, 1901.

(118) ———. 1905. La psychologie comparée est-elle légitime? Arch. Psychol. Genève, 5: 13–35.

(119) Clark University. 1899. Clark University, 1889–99; decennial celebration. Worcester, Univ. Press, 566 p.

(120) Cole, L. W. 1907. Concerning the intelligence of raccoons. J. Comp. Neurol., 17: 211:61.

(121) Davis, H. B. 1907. The raccoon: a study in animal intelligence. Amer. J. Psychol., 18:447–89.

(122) Dewey, J. 1896. The reflex arc concept in psychology. Psychol. Rev., 3:357–70.

(123) Diserens, C. M. 1925. Psychological objectivism. Psychol. Rev., 32:121–52.

(124) Dunlap, K. 1912. The case against introspection. Psychol. Rev., 19:404–13.

(125) ———. 1914. Images and ideas. Johns Hopk. Univ. Circ., 33:161–77.

(126) ———. 1916. The results of a questionary on psychological terminology. Johns Hopk. Univ. Circ., 35:587–639.

(127) Engelmann, T. W. 1882. Über Licht- und Farbenperception niederster Organismen. Pflügers Arch., 29:387–400.

(128) ———. 1888. Die Purpurbacterien und ihre Beziehungen zum Lichte. Bot. Ztg., 46: 661–9; 677–89; 693–701; 709–20.

(129) Evans, C. L. 1926. 2nd Ed. Recent Advances in Physiology. London, Churchill, 370p. Chap. 14.

(130) Fielde, A. M. 1901. Further study of an ant. Proc. Acad. Nat. Sci. Philad., 53:521–44.

(131) Forel, A. 1901. Die psychischen Fähigkeiten der Ameisen und einiger anderen Insekten. München, Reinhardt, 57p. Eng. Tr. Wheeler, 1904. Chicago, Open Court, 49p.

(132) ———. 1910. Das Sinnesleben der Insekten. München, Reinhardt, 393p.

(133) ———. 1921–23. Le monde social des fourmis du globe comparé à celui de l'homme. Geneva, Kündig, 5v. Eng. Tr. Ogden, 1928. New York, Putnam, 2v.

(134) ———. 1923. Die Medizin der Gegenwart in Selbstdarstellungen. (Autobiographical sketch with author's list of 118 references) 6:35p. (Criticism of Forel's view by Renning. 1919. Biol. Zbl., 39:35–7).

(135) Graber, V. 1884. Grundlinien zur Erforschung des Helligkeits- und Farbensinnes der Tiere. Prag, Tempsky, 322p. (Excellent summary of preference method work of Bert, Graber, Lubbock, etc.)

(136) Hachet-Souplet, P. 1900. Examen psychologique des animaux. Nouvelle méthode expérimentale de classification des espèces au point de vue psychologique. Paris, Schleicher, 162p.

(137) Haggerty, M. E. 1909. Imitation in monkeys. J. Comp. Neurol., 19:337–455.

(138) Hall, G. S. 1908. A glance at the background of genetic psychology. Amer. J. Psychol., 19:149–212.

(139) Hamilton, G. V. 1911. A study of trial and error reactions in mammals. J. Anim. Behav., 1:33–66.

(140) ———. 1916. A study of perseverance reactions in primates and rodents. Behav. Monog., 3:No. 2, 65p.

(141) Herrick, C. J. 1907. Comparative psychology. Pop. Sci. Mon., 70:76–8.

(142) Hess, C. 1912. Vergleichende Physiologie des Gesichtssinnes. Jena, Fischer, 299p.

(143) Hobhouse, L. T. 1901. Mind in Evolution. 3rd Ed. 1926. New York, Macmillan, 483 p. (Rev. 2nd Ed. Yerkes. 1917. J. Philos., 14: 154–60).

(144) Hodge C. F. and Aikins, H. A. 1895. The daily life of a protozoan. Amer. J. Psychol., 6:524 33.

(145) Holmes, S. J. 1911. The Evolution of Animal Intelligence. New York, Holt, 296p. (See rev. by Bohn. 1912. J. Anim. Behav. 2:447–51).

(146) Holmes, S. J. 1916. Studies in Animal Behavior. Boston, Badger, 266 p.

(147) Hunter, W. S. 1912. The delayed reaction in animals and children. Behav. Monog., 2:No. 1, 86p.

(148) James, W. 1904. Does consciousness exist? J. Philos., 1:477–91.

(149) Jennings, H. S. 1906. Behavior of the Lower Organisms. (Based on papers appearing from 1897–1905). New York, Columbia Univ. Press, 366p.

(150) Kinnaman, A. J. 1902. Mental life of two *Macacus rhesus* monkeys in captivity. Amer. J. Psychol., 13:98–148; 173–218.

(151) Kirkpatrick, E. A. 1907. A broader basis for psychology necessary. J. Philos., 4:542–6.

(152) Kline, L. W. 1898. The migratory impulse vs. love of home. Amer. J. Psychol., 10: 1–81.

(153) ———. 1898. A review of Thorndike's *An experimental study of associated processes in animals*. Amer. J. Psychol., 10:149–50.

(154) ———.1899. Methods in animal psychology. Amer. J. Psychol., 10:256–79.

(155) ———. 1899. Suggestions toward a laboratory course in comparative psychology. Amer. J. Psychol., 10:399–430.

(156) Köhler, W. 1915. Optische Untersuchungen am Schimpansen und am Haushuhn. Abh. preuss. Akad. Wiss., Phys. -math. Kl., Nr. 3.

(157) ———. 1917. Intelligenzprüfung an Anthropoiden. Abh. preuss. Akad. Wiss., Phys. -math. Kl., Nr. 1; in book form as Intelligenzprüfungen an Menschenaffen. Eng. Tr. from 2nd Rev. Ed. The Mentality of Apes, Winter, 1925. New York, Harcourt Brace, 342p.

(158) Kostyleff, N. 1914. Bekhterev et la psychologie de demain. Rev. philos. France Étrang., 77:147–69.

(159) Lashley, K. S. 1923. The behavioristic interpretation of consciousness. Psychol. Rev., 30:237–72; 329–53.

(160) Loeb, J. 1900. Comparative Physiology of the Brain and Comparative Psychology. New York, Putnam, 309p. (See rev. by Nagel. 1899. Zool. Zbl., 6:611–4).

(161) ———. 1905. Studies in General Physiology. Chicago, Univ. Press, 2v. (Eng. Tr. of collected papers. (1888–1903).

(162) ———. 1906. The Dynamics of Living Matter. New York, Columbia Univ. Press, 233p.

(163) Loeb, J. 1912. The Mechanistic Conception of Life. Chicago, Univ. Press, 232p. (See rev. by Angell. 1913. J. Anim. Behav., 3:464–8).

(164) ———. 1916. The Organism as a Whole from a Physico-chemical Viewpoint. New York, Putnam, 379p.

(165) ———. 1918. Forced Movements, Tropisms, and Animal Conduct. Philadelphia, Lippincott, 209p.

(166) Lubbock, J. (Avebury). 1882. Ants, Bees, and Wasps. New York, Appleton, 448p.

(167) ———. 1883. On the Senses, Instincts, and Intelligence of Animals, with Special Reference to Insects. New York, Appleton, 292p.

(168) Lukas, F. 1905. Psychologie der niedersten Tiere. Wien und Leipzig, Braumüller, 276p.

(169) Marshall, H. R. 1908. The methods of the naturalist and psychologist. Psychol. Rev., 15:1–24.

(170) Mast, S. O. 1911. Light and the Behavior of Organisms. New York, Wiley, 410p. (See rev. by Parker. 1911. J. Anim. Behav., 1: 461–3; reply by Mast. 1912. Id., 2:209–17).

(171) Mills, W. 1898. The nature and development of animal intelligence. London, Unwin, 307p. (See criticism by Whitman. 1898–99. Monist, 9:524–37).

(172) ———. 1899. The nature of animal intelligence and the methods of investigating it. Psychol. Rev., 6:262–74.

(173) ———. 1904. Some aspects of the development of comparative psychology. Science, 19:745–57.

(174) ———. 1906. A short chapter in comparative physiology and psychology. Trans. Roy. Soc. Can., 12:291–300.

(175) Morgan, C. L. 1891. Animal Life and Intelligence. Boston, Ginn, 512p.

(176) ———. 1894. Introduction to Comparative Psychology. 2nd Ed. 1906. New York, Scribner, 386p.

(177) ———. 1896. Habit and Instinct. London, Arnold, 351p.

(178) ———. 1900. Animal Behavior. London, Arnold, 344p.

(179) ———. 1905. Comparative and genetic psychology. Psychol. Rev., 12:78–97.

(180) ———. 1910. Intelligence in animals. Encyc. Brit. 11th Ed., 14:680–2.

(181) ———. 1924. The conditioned response. Bristol Med.-Chir. J., 41:165–79.

(182) NORMAN, W. W. 1899. Do the reactions of the lower animal against injury indicate pain sensation? Amer. J. Physiol., 3:271–84.
(183) NUEL, J. P. 1906. La psychologie comparée est-elle légitime? Réponse à M. Claparède. Arch. Psychol. Genève, 5:326–43.
(184) PARKER, G. H. 1896. The reactions of metridium to food and other substances. Bull. Mus. Comp. Zool. Harv., 29:105–19.
(185) ———. 1918. The Elementary Nervous System. Philadelphia, Lippincott, 229p. (Summaries of previous work).
(186) ———. 1922. Smell, Taste, and Allied Senses in the Vertebrates. Philadelphia, Lippincott, 192p. (Summaries of previous work).
(187) PAVLOV, I. P. 1906. The scientific investigation of the psychical faculties or processes in the higher animals. (Huxley Lecture) Lancet, 2:911–5.
(188) ———. 1927. Conditioned Reflexes. Tr. by Anrep. London, Oxford Univ. Press, 430p. Chap. I.
(189) PECHSTEIN, L. A. 1917. Whole vs. part methods in motor learning. Psychol. Rev. Monog., 23: No. 99, 80p.
(190) PECKHAM, G. W. and E. G. 1898. On the instincts and habits of the solitary wasps. Bull. Wisc. Geol. Nat. Hist. Surv., 2:245p.
(191) ———. 1905. Wasps, Social and Solitary. Boston, Houghton-Mifflin, 310p.
(192) PERRIN, F. A. C. 1914. An experimental and introspective study of the human learning process in the maze. Psychol. Rev. Monog., 16: No. 70, 97p.
(193) PIÉRON, H. 1915. L'attitude objective dans la psychologie moderne. Scientia, 17:119–33.
(194) ———. 1924. Psychologie zoologique. Traité de psychologie. Tome 2:635–702.
(195) PILLSBURY, W. B. 1917. The new developments in psychology in the past quarter century. Philos. Rev., 26:56–69.
(196) PORTER, J. P. 1904. A preliminary study of the psychology of the English sparrow. Amer. J. Psychol., 15:313–46.
(197) ———. 1906. Further study of the English sparrow and other birds. Amer. J. Psychol., 17:248–71.
(198) ———. 1910. Intelligence and imitation in birds. Amer. J. Psychol., 21:1–71.
(199) RIBOT, T. 1899. The intelligence of animals. The Open Court, 13:85–97.
(200) RICHARDSON, F. 1909. A study of sensory control in the rat. Psychol. Rev. Monog.,
(201) ROSENTHAL, J. 1905. Physiologie und Psychologie. Biol. Zbl., 25:713–20; 741–52.
(202) ROUSE, J. E. 1905. Respiration and emotion in pigeons. J. Comp. Neurol., 15:494–513.
(203) ———. 1906. The mental life of the domestic pigeon. Harv. Psychol. Stud., 2:581–613.
(204) SANFORD, E. C. 1903. Psychology and physics. Psychol. Rev., 10:105–19.
(205) SCHNEIDER, K. C. 1905. Grundzüge der vergleichenden Tierpsychologie. Biol. Zbl., 25:666–79; 702–13.
(206) SHEPHERD, W. T. 1910. Some mental processes of the rhesus monkey. Psychol. Rev. Monog., 12: No. 52, 61p.
(207) SMALL, W. S. 1899. Notes on the psychic development of the young white rat. Amer. J. Psychol., 11:80–100.
(208) ———. 1900. An experimental study of the mental processes of the rat. Amer. J. Psychol., 11:133–65.
(209) ———. 1900–01. Experimental study of the mental processes of the rat. II. Amer. J. Psychol., 12:206–39.
(210) SPAULDING, E. G. 1904. An establishment of association in hermit crabs, *Eupagurus longicarpus*. J. Comp. Neurol., 14:49–61.
(211) THORNDIKE, E. L. 1899. A reply to *The nature of animal intelligence and the methods of investigating it*. Psychol. Rev., 6:412–20.
(212) ———. 1911. Animal Intelligence. (Col. papers, 1898–1901). New York, Macmillan, 297p. (See rev. by Carr. 1912. J. Anim. Behav., 2:441–6; Morgan. 1898. Nature, 58:249–50).
(213) TITCHENER, E. B. 1897. 2nd Ed. An Outline of Psychology. New York, Macmillan, 352p.
(214) ———. 1898. A Primer of Psychology 2nd Ed. 1899. New York, Macmillan, 316p.
(215) ———. 1910. A Textbook of Psychology. New York, Macmillan, 565p.
(216) TRIPLETT, N. B. 1901. The educability of the perch. Amer. J. Psychol., 12:354–60.
(217) VERWORN, M. 1889. Psycho-physiologische Protisten-studien. Jena, Fischer, 218p.
(218) ———. 1894. Allgemeine Physiologie. Jena, Fischer, 584p. Eng. Tr. from 2nd Ed. Lee, 1899. London, Macmillan, 615p.
(219) VINCENT, S. B. 1912. The function of the vibrissae in the behavior of the white rat. Behav. Monog., 1:No. 5, 81p.
(220) ———. 1915. The white rat and the maze problem. J. Anim. Behav., 5:1–24; 140–

(221) WARDEN, C. J. and WARNER, L. H. 1927. The development of animal psychology in the United States during the past three decades. Psychol. Rev., 34:196–205.

(222) WARREN, H. C. 1918. Definitions and delimitations of psychological terms. Psychol. Bull., 15:89–95; 19:230–3; 22:370–4.

(223) WASHBURN, M. F. 1908. The Animal Mind. 3rd Ed. 1926. New York, Macmillan, 431p. (Rev. by de Laguna. 1918. J. Philos., 15:617–27; reply by Washburn. 1919. Id., 16:41–4; rejoinder by de Laguna. Id., 16: 296–300).

(224) ———. 1917. The last quarter century in psychology. Philos. Rev., 26:46–55.

(225) WASMANN, E. 1897. Vergleichende Studien über das Seelenleben der Ameisen und der höheren Tiere. Freiburg, Herder, 122p. Eng. Tr. 1905. St. Louis, Herder, 200p.

(226) ———. 1897. Instinct und Intelligenz im Thierreich. Freiburg, Herder, 94p. Eng. Tr. from 2nd Ed. 1903. St. Louis, Herder, 171p.

(227) ———. 1900. Einige Bemerkungen zur vergleichenden Psychologie und Sinnesphysiologie. Biol. Zbl., 20:342–50.

(228) WATSON, J. B. 1903. Animal Education. Chicago, Univ. Press, 122p.

(229) ———. 1907. Kinaesthetic and organic sensations: their rôle in the reactions of the white rat to the maze. Psychol. Rev. Monog., 8: No. 33, 100p.

(230) ———. 1908. Imitation in monkeys. Psychol. Bull., 5:169–78.

(231) ———. 1913. Image and affection in behavior. J. Philos., 10:421–8.

(232) ———. 1913. Psychology as the behaviorist views it. Psychol. Rev., 20:158–77. (See rev. by Titchener. 1914. Proc. Amer. Phil. Soc., 53:1–17).

(233) ———. 1914. Behavior: an Introduction to Comparative Psychology. New York, Holt, 439p. (See rev. by Thorndike and Herrick. 1915. J. Anim. Behav., 5:462–70).

(234) ———. 1916. The place of the conditioned reflex in psychology. Psychol. Rev., 23: 89–117. (See article *Behaviorism* 13th Ed. Encyc. Brit.)

(235) ———. 1917. An attempted formulation of the scope of behavior psychology. Psychol. Rev., 24: 329–52.

(236) ———. 1919. Psychology from the Standpoint of a Behaviorist. 2nd Ed. 1924. Philadelphia, Lippincott, 448p. (See rev. by Herrick. 1920. Psychobiology, 2:449–553).

(237) WEBB, L. W. 1917. Transfer of training and retroaction. Psychol. Rev. Monog., 24: No. 104, 90p.

(238) WEISS, A. P. 1924. A Theoretical Basis of Human Behavior. Columbus, Adams, 428p.

(239) WHEELER, W. M. 1910. Ants: Their Structure, Development, and Behavior. New York, Columbia Univ. Press, 663p.

(240) ———. 1923. Social Life among the Insects. New York, Harcourt, Brace, 375p.

(241) WHITMAN, C. O. 1898. Animal behavior. Biol. Lect. Wood's Hole, 6:285–338.

(242) ———. 1898–99. Myths in animal psychology. Monist, 9:524–37.

(243) WILTBANK, R. T. 1919. Transfer of training in white rats upon various series of mazes. Behav. Monog., 4: No. 1, 65p.

(244) WOODBRIDGE, F. J. E. 1905. The nature of consciousness. J. Philos., 2:119–25.

(245) ———. 1913. The belief in sensations. J. Philos., 10:599–608.

(246) WOODWORTH, R. S. 1899. The accuracy of voluntary movement. Psychol. Rev. Monog., 3:No. 13, 114p.

(247) WUNDT, W. M. 1892. 2nd Ed. Vorlesungen über die Menschen- und Thierseele. Leipzig, Voss, 495p. Eng. Tr. from 2nd Ed. Creighton and Titchener, 1894. London, Sonnenschein, 454p. Lec. 23, 24, 26, 27, 28.

(248) ———. 1896. Grundriss der Psychologie. Eng. Tr. from 7th Ed. Judd, 1907. Leipzig, Engelmann, 392p. Part IV—Psychic developments.

(249) YERKES, R. M. 1901. The formation of habits in the turtle. Pop. Sci. Mon., 58: 519–25.

(250) ———. 1902. Habit formation in the green crab, *Carcinus granulatus*. Biol. Bull., 3: 241–4.

(251) ———. 1903. The instincts, habits, and reactions of the frog. I. The associative processes of the green frog. Psychol. Rev. Monog., 4: (Harv. Psychol. Stud., 1:) 579–638.

(252) ———. 1905. Animal psychology and criteria of the psychic. J. Philos., 2:141–9.

(253) ———. 1907. The Dancing Mouse. New York, Macmillan, 290p.

(254) ———. 1914. The Harvard laboratory of animal psychology and the Franklin field station. J. Anim. Behav., 4:176–84.

(255) YERKES, R. M. 1916. The mental life of monkeys and apes. Behav. Monog., 3: No. 1, 145p.

(256) ———. 1917. Methods of exhibiting reactive tendencies characteristic of ontogenetic and phylogenetic stages. J. Anim. Behav., 7:11–28.

(257) YERKES, R. M. and HUGGINS, G. E. 1903. Habit formation in the crawfish and *Cambarus affinis*. Psychol. Rev. Monog., 4: (Harv. Psychol. Stud., 1:) 565–77.

(258) YERKES, R. M. and MORGULIS, S. 1909. The method of Pavlov in animal psychology. Psychol. Bull., 6:257–73.

(259) YERKES, R. M. and WATSON, J. B. 1911. Methods of studying vision in animals. Behav. Monog., 1: No. 2, 90p.

(260) YOAKUM, C. S. 1909. Some experiments on the behavior of squirrels. J. Comp. Neurol., 19:541–68.

(261) ZIEGLER, H. E. 1900. Theoretisches zur Tierpsychologie und vergleichenden Neuropathologie. Biol. Zbl., 20:1–16.

ANIMAL EVOLUTION

By AUSTIN H. CLARK
Smithsonian Institution

CREATIONISM, or the idea that living things have at some time in the past been created substantially in the same form as that in which we know them, has at the present time almost wholly given way to a belief in evolution, a doctrine which assumes the gradual development step by step of all the widely varying forms of life from an original form of simple structure.

Creationists and evolutionists alike have erred in considering life as a thing apart from the inorganic world, a manifestation not measurable in terms which otherwise are of universal application.

THE INORGANIC BASES OF LIFE

This is far from true. Just what life is we do not know. All living substance is composed of elements found also in inorganic substances, though in the bodies of animals and of plants these elements are combined in forms peculiar to living substance, or to the products of living substance. So we may consider life as the ability, confined to groups of certain complex carbon compounds, to increase in bulk indefinitely in such a way and in such varied forms as shall enable the increase to take place to the best advantage.

Increase in bulk, however, and diversity of form are perhaps not entirely disassociated from inorganic antecedents. In igneous magmas and in the minerals formed from them potassium and magnesium on the one hand and sodium and iron on the other tend to vary in correlation. That is, the igneous rocks and minerals which are high in potassium contain much magnesium and but little iron, while if the rock or mineral be dominantly sodic, iron will be high and magnesium low, if these be present.

This relationship between these pairs of elements appears to be carried over into the organic world, magnesium and potassium being essential to plant metabolism, the other pair being of minor importance, while iron and sodium are necessary for animal metabolism, magnesium and potassium very much less so.

In addition to this it has been pointed out that all organic forms may be interpreted as falling under one or other of the six systems of crystallization. All animals, the great majority of the protozoans and the early stages of the other types, are ultimately reducible to the isometric system, with three equal axes at right angles to each other, and throughout the animal kingdom there is a marked tendency for the adults of the more complex types to revert to this simple form.

Plants, on the other hand, are fundamentally reducible to the orthorhombic system, with three unequal axes at right angles to each other, or to the tetragonal system, with three axes at right angles to each other, two equal and the third longer or shorter. As a concrete example, the mints (Menthaceæ) may be said to have orthorhombic leaves and a tetragonal stem.

Sodium and iron and the isometric tendency, potassium and magnesium and the orthorhombic or tetragonal tendency,

characterizing animals and plants respectively, may be significant as the persistent relics of inorganic features, though we do not know that this is true.

Each animal or plant is an intricate complex of interrelated and coördinated chemical reactions continually taking place within a body so adjusted to the physical forces by which it is surrounded as to enable these chemical reactions to be carried on most advantageously.

First of all, therefore, an animal or plant is to be regarded as a natural laboratory wherein are continually carried on multitudes of chemical reactions made possible through constant replenishment from the air and from the soil of substances used up.

THE BUTTERFLY AND THE UNIVERSE

The intricate external interrelationships of such a chemical complex may be understood by a brief enumeration of the contacts of a butterfly in terms of the world taken as a whole.

Young butterflies are known to us as caterpillars. Caterpillars eat leaves—or at least most of them eat leaves. Leaves are produced by plants. In order to grow plants must be supplied with water. To them water comes in the form of rain. Rain is moisture condensed from the air passing in the form of winds above the earth. Most of the moisture gets into the air by evaporation from the surface of the sea, which covers seven-tenths of the area of the globe.

The connection between the oceans and the caterpillar chiefly depends on emanations from the sun which provide the energy by means of which the water is evaporated from the surface of the sea, the winds are made to blow, and the green substance in the leaves of plants is enabled to form organic out of inorganic substances.

Day and night, and the varying seasons of the year, are functions of the emanations from the sun combined with the spinning of the earth about its axis and its yearly course about the sun.

Weather and climate play an important part in the life of every butterfly, directly, and also indirectly through their action on the land and sea, sometimes thousands of miles away. For instance the alpine butterflies living on the mountain tops in central Asia depend on snow and rain brought in the form of water vapor by the higher currents of the air from the Atlantic Ocean across the plains of Europe and of western Asia.

The processes grouped under the general heading of geology play a most important part in the lives of all the butterflies. Their caterpillars must have leaves to eat. In order to produce the necessary leaves plants must have food. Plant foods mostly come from soils. Soils are formed from the disintegration of the rocks, which, under the influence of heat, cold, rain, and other factors, both physical and chemical, are continually breaking up and being washed away as muds or sands or gravels, which, lodging in the valleys, provide the necessary food for plants.

As caterpillars feed on plants, each on a special kind or kinds, female butterflies are expert botanists and always know exactly the right plant on which to lay their eggs. In addition, they are good zoölogists, for they are quick to recognize their enemies and are expert in avoiding them. At the same time, very many butterflies take a keen delight in pestering creatures weaker or less agile than themselves, and some of the larger ones will even dart at the smaller birds, sending them to cover.

The bodies of the caterpillars and of the butterflies show the most perfect adaptation to their diverse modes of life.

It is not necessary to carry this recital

further. From this brief statement it is evident that a butterfly depends for its existence on a very definite correlation and coördination of, and a most delicate balance between, all the cosmic forces; and every living thing has just as many and just as varied contacts as has a butterfly.

These simple facts, which seem almost self evident, must constantly be kept in mind in considering organic evolution.

REPRODUCTION AS A PHASE OF GROWTH

Another fact to be constantly remembered is that life is the ability inherent in so-called living things to increase in bulk indefinitely. With the delicate balance that exists between all living things and their environment, their dependence on certain restricted types of food to maintain the necessary chemical reactions and on delicate physical adjustments for the securing of that food, and to avoid serving as food for something else, how can this be brought about?

In the organic world the individual animal or plant is simply a phase in the unbroken continuity in the increase of living substance. The adult animal is always so adjusted to the environment in which it lives that it accumulates a surplus of its special complex of organic compounds. No adult animal can grow beyond a certain size without increasing maladjustment to the forces by which it is strictly circumscribed. But it can accumulate and store up material over and above its own special needs.

This material is released in the form of eggs or young or buds, or in some other form at or near the bottom of the scale through which the individual passes during its life cycle. Once it is released, this surplus substance, in the form of numerous units, runs the same course as the parent organism, resulting in an increase in the organic substance.

This oscillation through a wide range of limiting conditions, from eggs or young to adults, by which increase in total mass is effected by all living things, is extremely complicated. Its simplest form is seen in those minute creatures known as protozoans, which, when the maximum size possible for them is reached, simply divide in two; each of the two derivatives grows to the maximum efficient size, and then again divides. Its most complex form is to be observed in certain flies (Hippoboscidæ and *Glossina*) in which the females produce maggots, which immediately form a pupa, so that there is no pre-adult feeding stage.

In the first case, that is, among the protozoans, the growing young feed from the very first on the same substances that support the parents. In the second case, among the viviparous flies, the young are fed throughout their entire pre-adult existence, on special secretions formed within the body of the mother.

Between these two extremes there is every possible intermediate. The mammals—dogs, cats, etc.—and many other forms of life approach the hippoboscid flies; they are fed by a secretion from the mother until they are sufficiently developed to gather their own food, which in these cases is always like that of the adult stage. In other types of life, as illustrated by the reptiles and the gallinaceous birds, the egg is provided with a supply of food material sufficient to carry the young up to a stage when they can find or capture and assimilate the normal adult food. In still other forms of life, as especially in certain birds, the young are capable of feeding only on animal substances, while the adults are especially seed eaters. On the other hand, the tadpoles of our common frogs feed on vegetable detritus, but the adults feed on living animals, particularly insects. Some creatures feed only in the younger stages, and the adult

stage is entirely devoted to the preparation and the dissemination of the eggs. This is the case with the magnificent great moths of the family Saturnidæ, and also with various other insects in which in the adult stage the mouth parts are defective. In the majority of the flying insects most of the feeding is done in the wingless stages, the flying stage being devoted especially to propagation.

GROWTH AS A CHANGE OF TYPE

The growth of animals from the young to the adult stage is not a simple matter of increase in size, for with increasing size there is a corresponding change in all the relations to environment. Often this change is slight, as in dogs, cats and cattle, but more often it is very marked, as in the insects and in the sea invertebrates.

Most animals, therefore, must be considered not as a single type of creature of increasing size, but as a series of different and successive types each with its special range of limiting conditions, and each with its peculiar problems in securing food and in avoiding enemies which it must overcome in order to exist.

As an illustration I may mention that pretty little butterfly known in England as the large blue (*Lycæna arion*). On hatching from the egg the tiny caterpillars of this butterfly feed on the flower heads of the thyme. They are protected from their enemies by ants which constantly attend them, attracted by a honey-like secretion they produce. They are inveterate cannibals, and if two meet one always eats the other. Later they leave the thyme and, crawling down into the ants' nest, live wholly as carnivores preying on the larvæ of the ants. They are now no longer cannibals. They transform to pupæ in the ants' nest, and the adult butterflies crawl out through the ant passages.

This insect is first a vegetarian caterpillar living in the open, later a predaceous grub living under ground, and finally a butterfly. These three quite different forms require three quite different sets of internal and external chemical and physical adjustments.

The question of survival in each animal species is in the majority of types associated with the passage of the individual through more or less widely different types or forms as illustrated by this butterfly and, strange as it may seem, except for mammals, the dominant animals of the present day, both on the land and in the sea, are those in which there is the maximum diversity between the younger and the adult stages.

VARIATION

How is it possible for a single individual in its development to pass from one form into another wholly different in both internal and external chemical and physical relationships? And how is it possible for closely related types, like the large blue of England and our common blues, to have life histories which are almost wholly different?

The answer to this question is to be found in a study of variation. Every animal type at every stage varies in all directions from the normal form. The limit of variation as we see it is determined solely by the ability of the variants to survive under the conditions by which they are surrounded. Extreme variants are usually classed as aberrations, abnormalities or deformities, but in reality there are no such things in nature.

In our contemplation of the animals we are prone to regard any given individual as normal if it is similar to the majority of others of the same restricted species, but if it departs more or less widely from the form which we regard

as typical we consider it aberrant or abnormal.

But in the animal world no forms are really aberrant or abnormal. The individuals we regard as such are merely unusual under present day conditions. Let conditions change, and a so-called abnormal form in any animal may prove to be better fitted to exist and so may replace the present normal form. This may happen in the adults only, or in any or all of the younger stages.

As the chemical and physical relationships of animals are of two kinds, internal and external, variation may be induced either by internal or external causes, or by both together.

The significance of variation may be made clear by the citation of a few examples.

Among the vertebrates there are two well marked lines of deviation from the structural average, both of which are characteristic of certain types and also occur as deformities or abnormalities in others, in which they are incompatible with other features necessary for existence.

In all the back-boned animals there is a marked tendency toward a great enlargement of the hinder pair of limbs, with a corresponding reduction in the size of the anterior pair. This feature is characteristic of the frogs, dinosaurs, moas, ostriches and other birds, certain fishes, and such mammals as the kangaroos, rabbits and hares, jerboas and jumping mice, and others. It is a not infrequent "deformity" in cats and cattle, and probably in all other vertebrates; but in these it only appears occasionally, and the individuals so malformed usually die young, being unable to meet the competition of their relatives of the usual type.

A study of the malformed young of cats and cattle shows that in these animals there is a latent tendency to develop types resembling the rabbits or the kangaroos. A kangaroo-like cat, however, could not hold its prey, while the feet of a kangaroo-cow would be wholly unsuited for a leaping mode of progress. Nature constantly is striving to produce these creatures, which in the modern world are impossible anomalies.

Enlargement of the fore limbs at the expense of the hinder pair is characteristic of such birds as goatsuckers, frigate-birds and others, of the pterodactyls, of flying and certain other types of fishes, and of bats, most monkeys, and certain other types of mammals.

Among the butterflies individuals occasionally are found which are male on one side and female on the other. Sometimes the wings of a single individual are divided into irregular or more or less regular patches some of which show the male and others the female type of coloration. Many cases of hermaphroditism are also known from other insects, and from all the groups of vertebrates.

Hermaphroditic individuals in bisexual forms are abnormal only when judged by the standard of their parents. Viewed in their broader aspect they are not abnormal, but represent a recrudescence of a tendency everywhere present among the animals to unite both sexes in a single individual.

Such bisexualism is a characteristic feature of the individuals in a number of different types of animals, where its fixation as a normal feature is not incompatible with other economically necessary features.

Extreme variants range all the way from frequent to very rare. But every type of variant capable of existence seems to be recurrent in succeeding generations, and it has been found that some, at least, are strongly dominant when bred with the usual form.

The occurrence of many different kinds

of variants may be induced by unusual conditions surrounding the animal in the early stages, or they may be due to the influence of such conditions on the parents. Indeed, some forms of animal life are so very sensitive that it is almost impossible to produce the normal form under confinement. I have found this to be the case with our little carnivorous butterfly (*Feniseca tarquinius*).

By far the greater number of known variants are due to purely internal factors. These are much more numerous than is commonly supposed. For instance, in one of the common feather-stars from the Antarctic seas (*Promachocrinus kerguelensis*) no less than 54 per cent of all the young after they have reached the adult form show features never present in the fully grown. That is to say, more than half of all the young produced by this particular animal are of such a nature that there is no hope of their existence as adults under the conditions they must meet. These hopeless variants, however, all show features occurring normally in other types of crinoids found elsewhere.

The persistence of a variant type depends on two conditions. It must have an internal balance permitting it to function normally, and it must reach a situation where it may exist in the face of competition. If these two conditions can be met, life is possible for any variant, no matter how profoundly it may differ from its parents, and it becomes possible for it to reproduce its kind.

In the crustaceans the most frequent abnormality is a difference in the two sides, or an asymmetry, which may amount to a grotesque distortion in a large percentage of the young. But many of the hermit crabs have succeeded in making an asset of a distorted body, while other still more distorted types have found existence possible as parasites.

In the crustaceans deviation from the usual type has progressed so far as to give rise to such anomalies as the barnacles, and to a host of curious parasites of widely different sorts, one of which (*Thompsonia*) is simply a mass of structureless mycelium-like roots within the tissues of the host.

In the closely allied insects a difference in the development of the two sides is seldom noticed. But it is not infrequent. In raising butterflies individuals are often found with the wings of the two sides of more or less different shape. In nature these, as they cannot fly, or at least fly well, are eliminated as fast as they appear.

The ability to travel in a straight line is a necessity for all animals on land, since they must seek their food, or a food supply for their young. It is not a necessity for animals living in the sea, since if these cannot seek their food the water will do the work of bringing food to them. So any deviation from the usual body form of insects that involves a difference in the development of the two sides and thus hinders or prevents progress in a straight line, is incompatible with the existence of the individuals concerned, while in the crustaceans distorted individuals may somewhere find an economic niche where life for them is possible.

What is the significance of variation, and what is its effect on animal life taken as a whole?

WHAT IS A SPECIES?

Before we answer this we must first define a species. The accepted definition of a species is an assemblage of individuals which agree with each other in form, size, color and other characters, in one or more of which they constantly differ from related assemblages of individuals, which normally and freely interbreed, and which transmit to their offspring their proper characters unchanged, or with that little

modification which is due to conditions of environment.

This definition is much too narrow. It is simply a slight broadening of a definition of an individual, and contemplates primarily material in museum collections. Furthermore, it is based primarily upon vertebrates, especially birds and mammals, and scarcely applies to the other forms of life even as represented in museums.

What, then, is a species? That is difficult to say, for the different kinds of animals vary greatly in the interrelationships of the individuals and in their relations to allied types.

A species must be considered as represented by the so-called normal type plus all of its variants and aberrations, whether occurring naturally or induced by changed conditions.

In any kind of animal the normal type, so called, at every stage represents merely the present actuality. The variants and aberrations represent the potentialities, and with changed conditions any one or more of these may become an actuality, replacing the normal form, representing it in another region, or representing it in the same region under different ecological conditions.

THE THREE PATHS OF DEVELOPMENT

No true appreciation of animal life taken as a whole is possible without a consideration of animal development. All animals originate from single cells. Some remain all their lives as single cells, while in others the original single cell becomes a more or less complex mass of cells.

Assuming that the earliest animals, like those of the present day, began life as a single cell, there are three alternatives which subsequent development might follow. There is no reason for believing that these three paths were not followed simultaneously, that is, that animal life did not from the first develop in three divergent ways.

A single cell cannot increase in size beyond a certain point without serious interference with the chemical and physical interchanges on which life depends. On reaching the maximum size permitted by the chemical and physical restrictions, the animal cell divides into two; later these two divide each into two, becoming four, these four become eight, these eight sixteen, these sixteen thirty-two, and so on indefinitely.

In this process of division there are three paths that may be followed. As they divide the cells may separate from each other so that the individual animals always remain composed of a single cell. In other words, on the division into two of the original cell each half may separate from the other and become a separate animal half the size of the original. Further division would give rise to a corresponding number of entirely separate animals, all when they reach the maximum size increasing by simple division into two. The so-called single celled animals, or protozoans, illustrate this process.

But after division into two the cells might remain in contact, and this contact might be maintained through successive cell divisions. Here there are two alternatives. The cells may adhere more or less irregularly so that a poorly differentiated mass of cells results, the mass as a whole being more or less distinctly radial in symmetry. The result of such development is represented by the sponges.

But on the other hand cell division may take place by regular geometrical progression, the original cell dividing into two, four, eight, sixteen, thirty-two, and so on, until a hollow ball of cells (a blastula) is formed, which, by collapsing, would form

a two layered cup (a gastrula) with the axis passing through the center of the opening and of the opposite pole, and the walls the same in all the radii.

RADIAL SYMMETRY

If such an animal form should continue its development to the adult stage, following to its logical conclusion the preceding line of geometrical development, the result would be an animal radially symmetrical and composed of two layers of cells. Such an animal is represented by the hydra and allied creatures, the so-called cœlenterates.

We know that all animals begin life as a single cell which divides into two, and these derivatives continue to divide in the same way. Undoubtedly the original animal forms had a similar life history. But there is no logic in the assumption that the earliest animals were single celled creatures of the protozoan type. It is far more likely that from the very first the dividing cells would take all three of the courses outlined, complete separation, formation of an irregular mass, or formation of a geometrical body developing into a two-layered creature with radial symmetry.

While it is most reasonable to suppose that all three alternatives were realized from the start, if any of the three were to precede the others it would presumably be the development of a more or less formless sponge-like mass from which on the one hand single celled creatures were derived, and on the other the geometrical multicellular types.

As typical of the single celled animals let us take the amœba as the best known. As typical of the animals developing into a formless mass we may take the sponges. And as typical of the result of geometrical development we may take the hydra.

The amœba, the sponges and the hydra are all radially symmetrical. The amœba is composed of a single cell; when it has reached the limit of its growth from the economic viewpoint it divides into two. The sponges, with their systems of canals which penetrate the mass, are capable of almost indefinite growth without transgressing economic boundaries.

But with the hydra it is different. The hydra, or any creature similarly formed, must remain of a size suitable for the capture of its prey. There are four ways in which this may be done without interrupting a continuous increase in bulk. The animal may do as the single celled amœba does, divide into two, or even into more, by the formation of buds which separate off and grow into complete and independent animals. This process occurs in hydra, in the sea-anemones, and in the solitary corals. Or the animal may do as the sponges do and grow into a large, more or less radially symmetrical mass with the food collecting mechanism distributed over the surface, as in the case of the brain corals. Or the animal may form a bud which eventually develops into another individual remaining attached to the first, the second individual may in the same way produce a third, and the third a fourth, and so on, until a more or less geometrically arranged plant-like structure results bearing many individuals or polyps, as in the case of the stag-horn corals, red corals, sea-pens, sea-fans, and similar things.

Thus it is evident that the individual radially symmetrical animals repeat the same processes that are seen in the development of the single cell. That is, when the limit of size is reached they divide into two individuals which separate from each other; they divide into two individuals which remain attached in such a way that further division results in the formation of a more or less symmetrical mass; or they

divide into two individuals which remain attached in such a way that further development results in the development of a geometrically arranged assemblage.

BILATERAL SYMMETRY

There is still another alternative, which is also foreshadowed in the single celled animals or protozoans. These last, as we know them now, are mostly asymmetrical with a more or less definite anterior end. In the same fashion a multicellular animal may start to develop in radially symmetrical fashion, but during the course of its development lose the radial symmetry and become bilaterally symmetrical with an anterior or head end, toward which naturally the mouth and chief sense organs converge and at which the controlling nerve centers become assembled.

With a bilaterally symmetrical, more or less elongated form and a head end at which are situated the controlling nervous centers and sense organs and the mouth, and endowed with locomotion, an animal becomes independent of its immediate surroundings. It is able to search for food and thus to get sufficient nutriment to enable it to grow to almost any size.

What evidence is there that the bilaterally symmetrical animals have any connection with radially symmetrical types? The gastrula—the two layered cup—or its equivalent is found in all animals except those composed of a single cell, and those composed of an unorganized mass of cells—the sponges. The latter are singularly diversified in their early stages, but these never include a gastrula comparable to that in the other multicellular animals.

The gastrula is the pre-adult stage in the hydra, the sea-anemones, the corals, the sea-pens, and their allies. In all other animal types it is the stage at which divergence takes place in all directions. In the flatworms and in the roundworms the adults show a bilateral symmetry with much of the original radial symmetry still remaining, but in all the other forms of animal life all traces of radial symmetry are lost.

All animals arise from a single cell; therefore we say that the single cell is the fundamental feature of the structure of all animals. But if this is true, then it is equally true that the gastrula, or the radially symmetrical element, is the fundamental feature of the structure of all the bilaterally symmetrical animals.

Especially to be remarked in the strictly bilateral animals is the constant recurrence of features characteristic of the radially symmetrical forms, such as the formation of colonies, as in the polyzoans, and reproduction by budding or division, as in some starfishes and ophiurans, and in many other types.

The constant recurrence of these features may mean either of two things. There may be a natural tendency in every animal group to adopt independently a colonial habit and a propensity to reduplication by simple division of the body after the manner of the radially symmetrical types, or the constant reappearance of these features may be due to an inherent principle common to all animals and inherited from a common origin in which these features dominated.

Generally speaking the tendency for animal types to form colonies or to reproduce by budding is inversely proportionate to their activity; that is, the more active the animals, the less tendency there is to produce colonies, or to reproduce by buds or by division.

Among the crustaceans there is only a single type (*Thompsonia*) that may properly be considered as colonial, while relatively few reproduce by budding in the

early stages; all of these are sedentary forms. Among the insects a few types exhibit the phenomenon known as polyembryony—the formation of two or more larvæ from a single egg—but quite a number, as ants, bees, wasps, and termites, the last named radically different from the others and related to the cockroaches, form colonies which, although the included individuals are all separate, show unmistakable resemblances to cœlenterate and other colonies. In the vertebrates, all of which are of large size and therefore require a large amount of food, these phenomena have almost completely disappeared, as would be expected. The remarkable powers of reparation possessed by certain amphibians are possibly a remnant of reproduction by budding, while the ceratioid fishes with the diminutive males parasitic on the females might be considered as colonial in habit, though beginning life as two or more wholly distinct individuals.

Animal colonies may form a single unit which may acquire locomotor powers and act exactly as if it were a single animal. Examples of this are the colonial jelly-fishes known as siphonophores, of which the Portuguese man-of-war (*Physalia*) is an illustration, swimming colonies of tunicates (*Pyrosoma*), and crawling colonies of polyzoans (*Cristatella*).

Among animal types true radial symmetry is relatively rare. Most of the protozoans are more or less asymmetrical, and most of the cœlenterates or "radiated animals" also are to a greater or lesser degree asymmetrical.

A tendency toward radial symmetry, more or less marked, occurs sporadically throughout the groups of animals which are primarily bilaterally symmetrical. Thus the adult sea-urchins, sea-lilies and feather-stars, starfishes, brittle-stars and holothurians, making up the group known as the echinoderms, are usually more or less perfectly radially symmetrical, although when young all echinoderms are bilaterally symmetrical.

Among the single celled animals or protozoans some are attached and more or less radially symmetrical, like *Stentor* or *Vorticella;* others are attached and form colonies on the summit of a stalk, like *Codosiga* or *Epistylis;* others, as *Amœba*, are free living and capable of locomotion, but are sluggish and creep equally well in any direction; some float freely suspended in the water; while others are elongated and more or less bilaterally symmetrical and swim with great rapidity. Some are naked, while others form beautiful regular and complicated shells of lime or other substances, or rough agglutinated tubes of sand grains, or other forms of covering.

All of these varied characters are duplicated among the radially symmetrical animals, and again in those derived through a gastrula stage, this duplication being rendered possible because the great difference in size prevents direct competition.

We need not carry this recitation further. It would appear that among the animals taken as a whole every possible response to the physical environment occurs, and furthermore is repeated in widely different types whenever because of a difference in size or for other reasons there can be no direct competition.

We can scarcely doubt, therefore, that in the first place animal life taken as a whole forms a unit which is very closely knit, with the component types far more intimately joined each to the other than is commonly supposed, and in the second place that the majority of the obvious differences between the component types

are not inherent in the animals themselves, but are a direct response to their physical surroundings.

If we admit the fundamental unity of animal life, we also must suppose that every animal type bears a perfectly definite relationship to every other, not merely to one or two which are more or less similar in structure.

The developmental history of animals commonly is shown in the form of a branching tree-like figure, the branches representing types which are assumed to be anomalous and of dubious relationships. Such a delineation denies the essential unity of animals taken as a whole. It assumes an aimless and haphazard plan in animal development wholly contrary to what we find in the domain of physics and of chemistry which together form the basis of all organic life. A logical view of the interrelationships of animals must be one that does not run counter to what is evidenced elsewhere.

But is there any evidence to show that the development of animals is reducible to any orderly plan? Can the various animal types be so arranged as to show a logical relationship each with all the rest?

THE DEVELOPMENT OF BILATERAL FROM RADIAL FORMS

In tracing animal development we considered the single celled animals, or protozoans, the sponges, and the radially symmetrical animals. The occurrence of a gastrula stage in all bilateral animals was assumed to show their origin from the radial type. How could the development of the numerous types of bilateral animals from a radial progenitor proceed?

If colonial cœlenterate animals should develop a persistent and considerable defect in the ontogeny whereby the units lost their perfect radial symmetry and acquired a pronounced bilateral symmetry, this would give rise to animals of four main types which, though chiefly bilateral, would retain to a considerable extent evidences of the fundamental radial symmetry.

These four new animal types, intermediate between radially and bilaterally symmetrical animals, but nearer the latter, would take the form of:

(1) Bilateral animals constituting a linear, more or less unified, colony.

(2) Bilateral animals in which the colony formation is inverted, the budding off of the new units taking place within the original unit.

(3) Solitary bilateral animals each representing a dissociated cœlenterate unit.

(4) Bilateral animals with the colonial habit, though independent of each other.

These four types are all foreshadowed in forms occurring among the cœlenterates themselves, and furthermore in cœlenterates in which the radial structure is slightly modified, being not quite perfect, but symmetrical on either side of a plane passing longitudinally through the units; in other words, in radially symmetrical animals which have acquired a partial bilateral symmetry.

What could be more natural than that radially symmetrical animals with a partial bilateral symmetry would pass over into bilateral animals with a partial radial symmetry in all the different forms in which the existence of a creature with such a mixed symmetry is possible?

Among the animals of the present day all four of these chief intermediate types are represented.

(1) The tapeworms or segmented cestodes form a linear colony having continuous growth which is so very similar to the partially unified chain of young in the common jelly-fish (the so-called strobila of *Aurellia*) as to leave little

doubt of the fundamental similarity of type. The head end, or scolex, of the tapeworms is always radially symmetrical, but the body, composed of a chain of proglottids, is flattened and bilaterally symmetrical, although the difference between the so-called dorsal and ventral surfaces is but little marked.

(2) The parasitic flatworms known as flukes have a peculiar development which is essentially similar to the strobilization of the jelly-fishes, except that the buds are formed within the original unit instead of in a linear series. The flukes and their allies always retain obvious traces of radial symmetry, especially in the digestive and in the nervous systems.

Here we come upon a most important fact. In the radially symmetrical animals in which the polyps are of different types, each fitted to perform a different kind of work, these polyps take three forms. They are (*a*) nutritive, or sack-like, specialized for feeding, (*b*) reproductive,

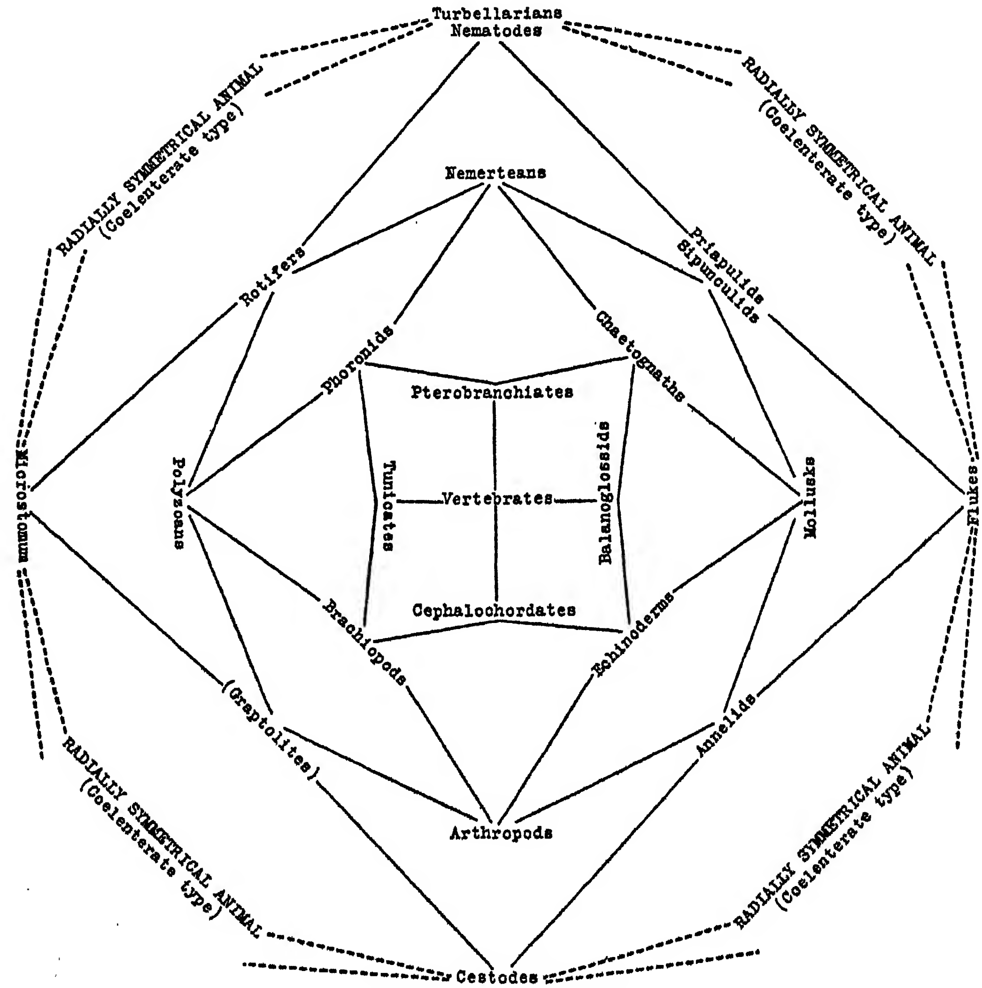


Fig. 1. Relations of the Various Types of Animal Structure

and (*c*) defensive, the defensive mechanism consisting of numerous cells containing a secretion and also a coiled tubule. These defensive polyps are probably to be classed as excretory with a secondary adaptation for defense rather than as primarily defensive.

What is the special significance of this? If in the formation of buds internally within the original unit these buds were of these three types into which the polyps of many of the cœlenterates typically are divided, nutritive, reproductive and excretory structures of a very definite sort would not only become internal, but would acquire a definite internal place and manner of origin.

In the animals possessing the internal structure known as a cœlome, the latter is divided into three sections, (*a*) the sack-like or perivisceral cœlome, (*b*) the reproductive or gonadial cœlome, and (*c*) the excretory or nephridial cœlome.

While we cannot trace any definite connection between the three divisions of the cœlome and the three types into which cœlenterate polyps are divided, yet the correspondence when considered in connection with the internal budding seen in the developing flukes, as contrasted with the linear budding occurring in the tapeworms, is so very striking that we can scarcely avoid the assumption that the cœlome arose from internal budding.

(3) The turbellarians and nematodes are solitary bilateral animals, both with distinct traces of radial symmetry in their nervous systems, and the turbellarians also with a more or less radially symmetrical digestive system. Each individual within these groups may be compared to a single cœlenterate polyp.

(4) Such turbellarians as *Microstomum* are single animals, each individual being comparable to a single cœlenterate polyp. But they divide in such a way as to produce a chain of similar attached animals, each of which is independent of the other and not an integral part of a more or less unified entity.

THE FLATWORMS AS CONNECTING LINK BETWEEN RADIAL AND BILATERAL FORMS

The tapeworms, the flukes, the turbellarians and *Microstomum* are all flatworms, and all are more or less closely related to each other. They all retain to a very considerable degree remnants of radial symmetry, as well as other cœlenterate features, while at the same time they are for the most part bilaterally symmetrical.

As they, and they alone, are structurally intermediate between the radially and bilaterally symmetrical animals, how can we avoid the conclusion that in some way or other they must form the connecting link between the two?

Prejudice always clouds our vision when it comes to parasites. All of the tapeworms and all of the flukes are parasites. They have therefore always been regarded as abhorrent creatures anomalous in structure, whose bizarre life history has been developed in accordance with their parasitic habits.

But nature does not produce anomalies. The reason that the tapeworms and the flukes are parasites is simply that their curious structure renders a free existence impossible for them under conditions as they are today. They occur only as parasites because to exist at all they must be protected by the body of a larger creature.

A parasitic branch from, for instance, annelid (as *Protomyzostomum*) or crustacean (as *Sacculina*) stock may become so changed as to lose nearly all vestiges of its true relationships. But however great

the change may be, such a branch never assumes features characteristic of other types of animals.

We cannot take refuge, therefore, in the supposition that the peculiarities of the tapeworms and the flukes are due to parasitism. They are instead features which are peculiarly adapted to a parasitic mode of life.

It cannot be assumed that these four types in exactly the form in which we know them now are the connecting links between the radial and the bilateral animals, but we can assume that they represent the only possible intergrading types.

COMBINATIONS OF THE FOUR FUNDAMENTAL TYPES

How can the other types of animals be derived from forms similar to the tapeworms, the flukes, the turbellarians and *Microstomum*?

We have drawn a developmental line from a single cell to a radially symmetrical animal. From the radially symmetrical animal we have drawn four radiating lines each ending in an animal type fundamentally different in structure from the other three.

One of these types is regularly segmented. The second shows internal differentiation suggesting the beginnings of cœlomic structures. The third is simple and solitary. The fourth is simple and colonial.

All four of these types had their origin in the same type, the radially symmetrical animal. They may therefore be presumed to be in a state of unstable equilibrium. The term unstable equilibrium here is used to mean a condition in which an animal type exhibits only a small range of the features found in the assumed ancestral form, the missing features being in abeyance, or existing in a latent form and prone to reappear if conditions render reappearance possible.

Unstable equilibrium predicates the existence of various stresses tending to cause the animal type to retrogress toward the original form through the reassumption of one or more of the missing features.

Unstable equilibrium therefore carries with it a constant tendency to readjustment, more or less complete, of the normal balance. So we are not surprised to find four more animal types each of which combines the characters of two of the four types just considered.

Thus there are (1) animals which are segmented like the jointed tapeworms, but possess the cœlomic structures foreshadowed in the flukes; (2) animals which are unsegmented like the turbellarians, but possess the cœlomic structures foreshadowed in the flukes; (3) solitary unsegmented animals like the turbellarians, with no cœlome, but with abundant asexual reproduction like *Microstomum;* and (4) segmented animals without a cœlome like the tapeworms, but less unified and with the continuous loss of the units as in *Microstomum.*

The segmented animals with a cœlome (1) are the annelidan or segmented worms; the unsegmented animals with a cœlome (2) are the priapulids and sipunculids; the solitary animals with no cœlome but with abundant asexual reproduction (3) are the rotifers; and the animals without a cœlome forming colonies of separate individuals (4) are undoubtedly the graptolites.

Through this readjustment each of the new animal types has combined within itself the features of two of the original types. But since in each of these new types two of the four chief features still are absent, there continues to exist a condition of unstable equilibrium as compared with the radial ancestor.

A second readjustment of the same nature as the first would be inevitable. This would result in the appearance of four different types, each of which would combine the characters of two of the preceding types, and of three of the types first mentioned.

Three such intermediates seem to be clearly indicated, in (1) the polyzoans (or bryozoans), colonial and not at all, or very imperfectly, cœlomate, between the rotifers and the graptolites; (2) the arthropods (insects, crustaceans, spiders, etc.) with a segmented body like that of the annelids, but divided into two or three units showing division of labor (in the insects one, the head, controlling and directing, one, the thorax, locomotor, and the third, the abdomen, performing the digestive, reproductive, and other vital functions) as in an animal colony, with a poorly developed cœlome, with abundant traces of asexual reproduction (polyembryony, parthenogenesis, fragmentation of larvæ, etc.), with a tendency to form colonies showing a division of labor among the (dissociated) individuals (as in the Hymenoptera and the termites), and sometimes even forming plant-like colonies (*Thompsonia*); and (3) the mollusks, always solitary, like the priapulids and sipunculids, with a highly developed cœlome, and with traces of segmentation (in the larvæ) suggesting the annelids. The last (4) group should be solitary, with a cœlome, without well developed segmentation, and with an indication of colonial structure. It is possible to place the nemerteans here, on the assumption that their remarkable powers of reparation are in reality related to budding and recreation of individuals of the cœlenterate type.

There is still a condition of unstable equilibrium, for in each of these four groups one of the original elements is lacking. A third readjustment would be necessary to recombine all of the main features characteristic of each of the original four types.

Four animal groups appear to be the result of such a readjustment. (1) The echinoderms combine a reduced body consisting of five half segments more or less of the arthropod type with a highly perfected cœlome as in the mollusks. (2) The arrow-worms or chætognaths suggest a relationship with the mollusks, and also with the nemerteans. (3) The phoronids suggest a relationship with the polyzoans, although the colonial habit is reduced to the budding off of new individuals, and have a well developed cœlome as in the nemerteans. (4) The brachiopods or lamp-shells suggest both the polyzoans and the shell-bearing arthropods.

While by this third readjustment all the four original features are recombined in each animal type, the balance between them is imperfect, for in each case the influence of one of these features is greatly overshadowed by the influence of the other three.

A fourth readjustment would correct this imperfect balance and result in the appearance of four animal types all very much alike.

There are four types which seem to belong here, the tunicates, the cephalochordates, the balanoglossids, and the pterobranchiates. The tunicates seem to be in line with the polyzoans, while they also suggest both the brachiopods and the phoronids. The cephalochordates clearly stand in the cestode-arthropod line, and at the same time show unmistakable affinities with the echinoderms. The balanoglossids, with no trace of asexual reproduction, may be considered as in line with the flukes and mollusks, and between the chætognaths and the echinoderms.

The pterobranchiates seem to fall between the chætognaths and the phoronids.

These four groups are much more closely similar to each other than any of the other series of four groups except the very first. While the first four groups all agreed in having a considerable degree of radial symmetry, the last four groups agree in the possession of a highly developed notochord.

These four groups possessing a conspicuous notochord are, though entirely distinct, so very close to each other that a fifth readjustment would presumably give a final type in which all of the four chief features of the original types would be reunited in the economically most perfected form, and the balanced adjustment of the original radiate progenitor would be once more attained.

The vertebrates appear to occupy this central place. In them we are able to recognize the segmentation of the cestodes, annelids and cephalochordates, combined with the cœlomic structures first indicated in the flukes, both enclosed in the undivided body characteristic of the turbellarians, which is provided with limbs possibly to be considered as having had their ultimate origin in budded units.

In the course of the various readjustments which culminated in the reëstablishment of the original balance in the vertebrates, numerous secondary features, such as the visual and other sense organs, appendages of different kinds, diverticula and other outgrowths from the enteric canal, chitinous and calcareous skeletons, etc., all of which features are found in a rudimentary form in the cœlenterates, attained an extraordinary development, so much so as often to overshadow and almost completely mask the fundamental characters.

THE FOSSIL RECORD

If this is a true delineation of the facts, it would naturally follow that at its very first inception on the earth animal life assumed essentially the form in which we know it now, for the various readjustments leading from the radial type of animal to the recombination of its characters in a seemingly wholly different form in the vertebrates would presumably be simultaneous, or very nearly so.

What can we learn in regard to this from the fossil record?

The earliest aquatic fauna that we know, that of the Cambrian rocks, was in its broader aspects singularly similar to the aquatic fauna of the present day. Every one of the numerous component species falls at once within a definite phylum as outlined by the living forms, and in a definite class within that phylum. Many of the species can be recognized as members of families still existing, while a few may be assigned even to recent genera.

In Cambrian times crustaceans were represented by phyllopods, trilobites and merostomes; among the echinoderms there were crinoids, cystideans, and elasipod holothurians; chætognaths, brachiopods and graptolites were present; of the annelids we know polynoids, nereids, gephyreans, and *Tomopteris*-like forms; of the mollusks there were pteropods and gastropods; and there were sea-anemones and other cœlenterates, and sponges.

As a supplement to this varied Cambrian fauna, we know from the Ozarkian rocks cephalopods and bivalve mollusks, and from the Ordovician polyzoans, sea-urchins, brittle-stars, starfishes, and fishes. There is no evidence that these were not also present in the Cambrian.

The significance of this imposing list of

Ordovician and pre-Ordovician animals becomes more evident if we contemplate the missing types, which are the following: the ctenophores, flatworms and roundworms, rotifers and gastrotrichas, priapulids and sipunculids, heteropods, archiannelid, oligochæte, myzostomid, hirudinid and onychophorid worms, nemerteans, phoronids, insects, pterobranchiates, balanoglossids, tunicates, and vertebrates other than fishes.

Except for the insects and the vertebrates, which are primarily terrestrial, all of these various types are soft bodied creatures which cannot reasonably be expected to occur as fossils, since they can only be preserved as such by the merest accident.

This long list of animal types represented by the fossils in the Cambrian and immediately succeeding rocks can have only one meaning. It shows conclusively that as far back as Cambrian time the status of the animal world was, in its broader features, just what it is today.

So we see that the fossil record, the actual history of the animal life upon the earth, bears us out in the assumption that at its very first appearance animal life in its broader features was in essentially the same form as that in which we know it now.

Of course it is quite likely, indeed it is most probable, that animals existed long before the commencement of the fossil record. But in this case, judging from the correspondence between the animals of the Cambrian and those of the present day, we may safely predicate a similar correspondence between the animals of the Cambrian and those of a more distant past.

EVOLUTION WITHIN THE MAJOR GROUPS

Thus so far as concerns the major groups of animals, the creationists seem to have the better of the argument. There is not the slightest evidence that any one of the major groups arose from any other. Each is a special animal complex related, more or less closely, to all the rest, and appearing, therefore, as a special and distinct creation.

But within each major group we see a very different picture. Here the fossil record shows a constant change from one horizon to another. These successive variations are probably simply indications of a direct response to physical alterations in environment favoring now one type or subtype, now another.

This continuous alteration in the elements within the various groups is what is commonly known as evolution. It is perhaps best illustrated in the vertebrates, since these are the most familiar of the animals.

The evolution of the reptiles from the Carboniferous to the end of the Cretaceous, and of the mammals from the end of the basal Eocene to the present day, or rather to the period just past (Pleistocene), forms a story of most absorbing interest. Here we can trace the gradual development from comparatively insignificant beginnings to a wonderful flowering of specialization and perfection.

So much has been written on this subject, especially in recent years, that it seems unnecessary here to pursue it further.

But it is well to emphasize that every evolutionary line has certain gaps; some have these gaps large and broad, while in others (as in the horses) the gaps are relatively small. These gaps probably are largely natural, and not due to a deficiency in the record. They indicate the continuation of the phylogenetic line through variants showing a more or less wide departure from the normal type which happened best to meet the conditions of the time. We observe plenty

of such variants whenever we raise any kind of animal in quantity.

GIANT FORMS

One of the curious features connected with the evolution of the animals in practically every major group is the development of giants, or of strange and bizarre forms, which suddenly disappear leaving no successors.

In raising any form of animal life individuals of unusual size are frequently encountered. For instance, in many of our moths and butterflies giants and dwarfs are very readily produced. It is idle to suppose that these do not occur as frequently, or almost as frequently, in nature.

But if this is true, then we have an adequate explanation of a curious phenomenon characteristic of successive fossil types in many different groups. It is often to be noticed that in successive geological horizons animals of a certain type will increase in size, at the same time departing more and more widely from their immediate relatives, until suddenly they disappear.

Since protection from predaceous enemies and from competitors of their own kind usually is best afforded by increased size and strength, it is to be expected that of all the infinite types of variants giants are perhaps the most likely to persist.

But increase in size means a corresponding decrease in the number of individuals in the area inhabited, since each individual requires a larger proportion of the food supply. Decrease in the number of individuals means a corresponding decrease in the number of variants, which become simply isolated abnormalities, and hence results in a gradual fixation and stabilization of the type through inability to change.

Once fixed and stabilized through reduction to a point where variants are simply sporadic and wholly isolated individuals, an animal type becomes wholly dependent on the maintenance of conditions as they are, and any change in these conditions results in its extinction.

The reason why animal types have persisted through succeeding geological ages in the smaller and more generalized forms is simply because in these there are always variants in sufficient numbers so that changing conditions may be met by the development of suitable forms from among these variants.

As giants require a very large amount of food it would seem that they should appear particularly within the animal groups capable of active locomotion and also with unusual ability to see or hear or both. This is indeed the case. The most spectacular of the giants of the past are to be found among the crustaceans and the insects, the cephalopod mollusks, and the vertebrates. The giants of the modern world are to be found in the same groups.

In conclusion we may say that while in many of the numerous major groups of animals we can demonstrate a constant change from age to age, evidenced by an increase in diversity and a more delicate adjustment to environment, among these major groups themselves we can see no fundamental change whatever. Ever varying in the finer details of its manifestations, in its major features animal life has from the very first remained unchanged.

LIST OF LITERATURE

(*Editorial Note:* In lieu of a complete bibliography, which would obviously be too extensive to print in of his own papers, a perusal of which will indicate the steps by which he arrived at the conclusions set

earlier papers form the connecting link between Dr. Clark's ideas and those of other zoologists.)

The steps in the evolution of animals. Journ. Washington Acad. Sci., vol. 11, No. 9, May 4, 1921, pp. 207–208.

A new classification of animals. Bulletin de l'Institut océanographique, Monaco, No. 400, September 20, 1921, pp. 1–24.

The evolution of the animal body. Journ. Washington Acad. Sci., vol. 12, No. 2, January 19, 1922, pp. 25–28.

Animal evolution. Proc. Nat. Acad. Sci., vol. 8, No. 7, July, 1922, pp. 219–225.

The origin of the vertebrates. Journ. Washington Acad. Sci., vol. 13, No. 7, April 4, 1923, pp. 129–138.

A comparative study of the most ancient and the recent marine faunas. Journ. Washington Acad. Sci., vol. 14, No. 21, December 19, 1924, pp. 487–491.

Observations on animal coloration. Scientific Monthly, vol. 20, No. 4, April, 1925, pp. 341–344.

Animals of Land and Sea. D. Van Nostrand Co., New York, 1925. Chapman and Hall, Ltd., London, 1926. Second enlarged edition, D. Van Nostrand Co., New York, 1927.

Animal voices. Scientific Monthly, vol. 22, January, 1926, pp. 40–48.

The biological relationships of the land, the sea, and man. Science, new series, vol. 65, No. 1680, March 11, 1927, pp. 241–245.

Geography and zoölogy. Annals of the Assoc. of American Geographers, vol. 17, No. 3, September, 1927, pp. 101–145.

THE METABOLISM OF INSECTS

By MARY HONORA SAYLE

Zoology Laboratory, University of Wisconsin

INTRODUCTION

INSECTS, because of their abundance and wide variety in form and structure, have proved to be interesting animals for observation and study. From the naturalist, we have learned much about their habits. The entomologist has classified this large group of animals and has contributed to our knowledge of insect anatomy and physiology. In the more recent years insects have been used in desiccation studies, and a great deal has been written about their ability to withstand drying. The question of the effects produced on them by high temperatures is one which has received the attention of biologists for many years. The older workers were interested chiefly in the determination of the so-called "upper thermal death points." A résumé of their observations is given by Davenport (8). Spallanzani (29) as early as 1787 wrote about the tolerance of insects to high temperatures. He determined the death points of flies, silkworm and butterfly larvae, and the larvae of the mosquito. These forms ranged in their high temperature tolerance from 37.5° to 43.5°C. Plateau (22) determined experimentally the thermal death point of a number of fresh water insects known to occur in thermal waters as well as in ordinary ponds and streams. The unacclimatized animals were kept in water, the temperature of which was gradually raised. Roedel (24) determined the ultra-minimum temperature of such forms as the honey bee and house fly. The house fly can resist −12°C. for five minutes and −5° for 40 minutes. The work done on temperature tolerance and acclimatization is interesting. A review of this subject with reference to high temperature is given by Brues (6).

HISTORICAL

More recently a number of biologists and physiologists have been interested in the metabolism of insects. Are insects affected by changes in temperature, light, and food supply? Investigators have found that their life processes are markedly affected by environmental changes. The metabolic processes taking place inside the body of an animal can be measured in the respiratory exchange of the animal by ascertaining either the oxygen consumption or the carbon dioxide output. From the results of various investigators it is of interest to note that the respiratory rates for insects are considerably higher than those of other animals.

Although a number of present day workers are interested in the metabolism of insects, we must note that the problem is not a new one. Spallanzani (30) made a number of observations on the larvae, chrysalides, and adults of silkworms, flies, bees, and wasps. He observed that the respiratory exchanges of the larva and imago were two or three times greater than those of the chrysalid. His numerical results have been branded as "not trustworthy," but we remember him as a pioneer in this field of research.

It is interesting to note that about 1830 the investigators were beginning to improve their technique. They were changing the methods of introducing oxygen into the animal chamber; they were finding new ways of securing airtight compartments. In general, apparatus was the big issue and Treviranus quite boldly criticized the methods and apparatus used by Sorg (27). Treviranus (32) studied the gaseous exchange of various animals, including some insects, such as butterflies, moths, flies, and beetles. He calculated the oxygen consumption per kilogram per hour for one of the beetles at a temperature of 13–15°C. In addition he measured the oxygen consumption and carbon dioxide output of three bees at 11.5°C. He found that the honey bee absorbed more oxygen at 27.5° than at 14°C.

Newport (19) studied the carbon dioxide output of insects in various stages of development. He found that the chrysalis of a certain butterfly produced less carbon dioxide than did the larva or the full-grown insect. Spallanzani had previously made this same observation.

In the classical work of Regnault and Reiset (23) no reference is made to temperature. They found that 2.62–2.82 grams of carbon dioxide were given off per day by 100 grams of May-beetles and 2.31–2.58 grams of oxygen consumed, giving a respiratory quotient of 0.82–0.79. (Respiratory quotient: Ratio of the number of molecules of carbon dioxide formed in oxidation, to the number of oxygen molecules used.) These investigators found that the silkworm chrysalid consumed one tenth as much oxygen per gram of body weight as did the earthworm.

Bütschli (7) studied the effect of temperature upon the gaseous exchange of the cockroach fed on different substances. A rise in temperature was followed by a regular rise in gaseous exchange. At 15°C. the gaseous exchange was twice as great as at 4°, and at 32° it was seventeen times greater than at 3°. Bütschli's findings were in the main confirmed by Vernon (33), although the latter's figures run somewhat higher than Bütschli's. Vernon measured the milligrams of carbon dioxide given off by the cockroach at 2°, 10°, 20°, and 30°C.

Loeb (15) used the chrysalides of certain butterflies and moths to determine the effect of light on carbon dioxide production. He found that it had no influence on the output and concluded that its effect on carbon dioxide production was due to an increase in muscular activity.

Many experiments have been performed on the gaseous exchange of silkworms. Of these the outstanding ones are those of Luciani and Piutti (18), Luciani and Lo Monaco (17), and Farkas (10). Luciani and Piutti found that at 10° the eggs gave off three times as much carbon dioxide as at 0°C. During incubation the respiratory quotient approached unity. At the time of hatching, the carbon dioxide output went up. Luciani and Lo Monaco found in silkworm larvae that there was a decrease of carbon dioxide during rest and a rise of carbon dioxide output during activity. The latter workers were not concerned with the influence of temperature upon the gaseous exchange. From the numerical results of these investigators it was calculated that a silkworm larva gives off 378 cubic centimeters of carbon dioxide per kilogram per hour at room temperature. Farkas determined the gaseous exchange of the eggs and of the larvae at the moment of hatching. The gaseous exchange was high at hatching, but gradually decreased with advancing age.

Sosnowski (28) studied the gaseous exchange of larvae and chrysalides of flies. He did not mention at what temperature

these experiments were carried out. He found that, in general, the carbon dioxide output decreased as the larvae approached the chrysalid stage. In the pupa the carbon dioxide output generally decreased one third to one fourth and rose again. Weinland (36), in his studies on the blow fly, utilized the gaseous exchange of the organism as a basis for estimating the chemical changes occurring during metamorphosis. He found that the larvae liberated ammonia, whereas in the pupae uric acid was produced. His experiments with metabolism in general indicate a markedly low carbon dioxide output at the beginning or early stages of pupation, which is followed by a period of rest. In later stages, however, an increase in the gaseous exchange of the organism took place. Tangl (31) obtained results from metabolism experiments on the silkworm similar in many respects to those of Weinland.

Parhon (21) studied the influence of temperature on the gaseous exchange of bees in the various seasons. She used thirty grams of bees—about six hundred insects—and found that with the advent of summer the exchange increased with rising temperature from 10 to 37°C., but decreased at a temperature of 40 to 45°. She concluded from these observations that the bees must possess a heat-regulating mechanism. Parhon also made observations on the gaseous exchange of flies, which, she found, rose regularly with increasing temperature, following very closely van't Hoff's Law. (For an increase in temperature of ten degrees centigrade, the rate of any reaction is approximately doubled or trebled.)

Slowtzoff (26) observed the influence of temperature on the gaseous exchange of insects, principally ants and manure beetles. He found that the exchange went up with rising temperature, but that an interval of twelve degrees existed, during which it remained constant. This interval lay between 12 and 24° for the manure beetle and between 20 and 34° for the ant. The respiratory quotient was higher for the ant than for the manure beetle.

Von Brücke (34) and von Linden (35) worked with the chrysalides of several butterflies. The former observed that the carbon dioxide output rose with rising temperature. Von Linden found that the respiratory quotient during the night was 0.76 and during the day only 0.66.

Battelli and Stern (2) observed the oxygen consumption and carbon dioxide output at different temperatures for the May-beetle, and for all stages in the metamorphosis of the silkworm and the fly. Adult flies consumed the most oxygen and gave off the most carbon dioxide of all the stages studied. These workers noted a decrease in the respiratory exchange when the temperature was raised beyond a certain limit. They found, furthermore, that the exchange usually increased in the first few hours at a high temperature and regained the normal or fell to a lower level later. Krogh (13) showed that in a number of forms and over nearly the whole range of temperature at which normal development took place the velocity of embryonic development was a linear function of the temperature. Krogh determined the carbon dioxide output of the chrysalides of the beetle, *Tenebrio molitor*, at different temperatures from 21° to 33°C. The results indicated that the total metabolism, so far as that can be judged from determinations of carbon dioxide exhalations, was constant over the range of temperatures investigated. There was no optimum temperature for the pupal development. The relation between the temperature and the average carbon dioxide production could not, therefore, be expressed satisfactorily by

van't Hoff's formula, but between 20.9° and 27.25°C. the increment in carbon dioxide production was proportional to the increase in temperature, and above 27° it decreased, as did the velocity of development increment.

Loeb and Northrop (16) found that the duration of life of fruit fly (*Drosophila*) cultures was a function of temperature, the insects living longer at lower temperatures. They also found that the life of *Drosophila* was normal only at temperatures above 10° and below 30°C. At 5° or less the duration of life of the adult was less than a week, while at 15° it was 92.4 days. At temperatures above 27.5° the coefficient for the rate of growth became negative. Temperatures beyond the normal range were incompatible with the life of the organism. They also found that the nature of the food influenced the duration of life and that an adequate food supply was necessary for work on the influence of temperature.

Allee and Stein (1) studied the carbon dioxide output of May fly nymphs in relation to light. Changes in metabolism accompanied changes in light reactions. Nymphs positive to light had higher metabolic rates than the negative nymphs. Negative nymphs when exposed to light gave off more carbon dioxide. In conditions of depressed metabolism, insects were negatively phototropic and vice versa.

Bodine (3) made an excellent study of the water content and the rate of metabolism in grasshoppers. These insects responded to temperature changes as did other cold-blooded forms; that is, increased temperature caused increased respiratory rates. Carbon dioxide determinations were made using single animals and each determination extended over a period of thirty minutes to one hour. There was a difference in carbon dioxide output according to the species, the difference being correlated probably with its mode of life. Active species had a higher respiratory rate than more sluggish types. The rate of carbon dioxide output was higher for animals lighter in weight and decreased progressively as the animals increased in body weight.

Bodine found that the amount of carbon dioxide given off by the grasshoppers decreased during successive periods of starvation. During the early period this decrease was rather slight and gradual, but later marked drops were noted. This decided decrease was due probably to the fact that at this time all residual food in the intestine had been utilized and body reserves alone were being used. Bodine found that after feeding starved individuals an increase in the rate of carbon dioxide output was evident.

Dirken (9), working on the cockroach, observed that the oxygen consumption was influenced by temperature, but not in the sense stated by van't Hoff's Law. As the temperature varied, "the gaseous exchange was probably modified by influences from the nervous system." More carbon dioxide was consumed in initial exposures to high temperatures than in exposures hours later to the same temperature. He suggested an adaptation in the gaseous exchange by the body cells.

Bodine (4) made carbon dioxide determinations on both hibernating and growing grasshoppers at the same temperature. The rates of carbon dioxide output for hibernating animals at 0–8°C. were noted, being an eighth to a tenth of the rate at room temperature, 20°C. The rates of carbon dioxide output in hibernating animals at room temperature remained higher than in growing animals, suggesting that the animals remained young throughout the period of hibernation. Bodine and Orr (5) studied the respiratory

metabolism of the fruit fly, *Drosophila*. Ten pupae were used at one time, and determinations of carbon dioxide output were made on successive days. They found that the weight decreased during pupal development and that the oxygen intake and carbon dioxide output decreased on the second day of pupal life and then gradually increased up to hatching.

Fink (12) found that the carbon dioxide output of potato beetles throughout the progress of hibernation invariably indicated a reduced metabolic activity, in some respects comparable wih that of starving animals. In the latter, however, "the velocity of reaction of the life processes continues to function most actively and reserve substances are rapidly depleted, a condition eventually leading to the death of the animal. In the [former] most of the life activities are considerably depressed and nutrient material is, therefore, used sparingly." With older beetles the metabolic activities were also extremely reduced, but not to the extent met with in hibernating or starving forms. Fink (11) in another investigation used the eggs and pupae of ten different species of insects in his study of metabolic rates. His experiments showed a greater amount of energy change during embryonic development as compared to the energy developed during metamorphosis. This was shown by the greater carbon dioxide output and by the oxygen intake. Low respiratory quotients were obtained during the embryonic and pupal development of insects, resembling similar low quotients obtained with hibernating forms.

Northrop (20) made another study of the metabolism and of the duration of life of cultures of *Drosophila* and found that more carbon dioxide was given off at 15°C. than at 26° or 30°, when both cultures were in the dark, and that more carbon dioxide is evolved in light than in darkness. This effect of light on carbon dioxide production has been shown earlier by Loeb (15) to be due to an increase in muscular activity, since insect pupae were not affected. Quite high light intensities have no effect on the duration of life of fruit flies, whereas numerous investigators have shown that illumination markedly increased the carbon dioxide production. The duration of life does not seem to be determined by the time required to produce a limited amount of carbon dioxide.

Perhaps the most useful compilation of data on metabolism is to be found in Krogh's (14) monograph on "The Respiratory Exchange of Animals and Man." This includes the results of several original experiments on insect pupae, particularly on chrysalides of the beetle, *Tenebrio molitor* (13).

THE METABOLISM OF DRAGON FLY NYMPHS

In a previous paper (25) the writer discussed in detail the effect of starvation, darkness, and temperature upon the carbon dioxide output of one of the dragon fly nymphs, *Aeshna umbrosa*. The adult dragon fly or "darning needle" is well known to almost every one, but fewer people are acquainted with the immature stage, which spends this period of its life cycle in the water, breathing by means of rectal gills. These nymphs are easily obtained and live successfully under general laboratory conditions. They offer especially desirable material for the study of respiration in a truly aquatic form. The nymphs used in the study were collected at the same time and from the same creek and were all approximately the same age. Three sets of ten insects each were used in each type of experiment and the results averaged and graphically shown.

The apparatus used by the writer was essentially the same as has been used by

other investigators. It consisted of a closed system of chambers and tubes, through which a circulation of air was maintained by means of a small air pump. The apparatus was run over a period of five hours for each experiment, and the air in the circuit was bubbled through barium hydroxide, which precipitated the carbon dioxide as barium carbonate. The excess of barium hydroxide was titrated with hydrochloric acid, using phenolphthalein as indicator. At the end of each experiment, carbon dioxide determinations in milligrams per gram insect per hour were made.

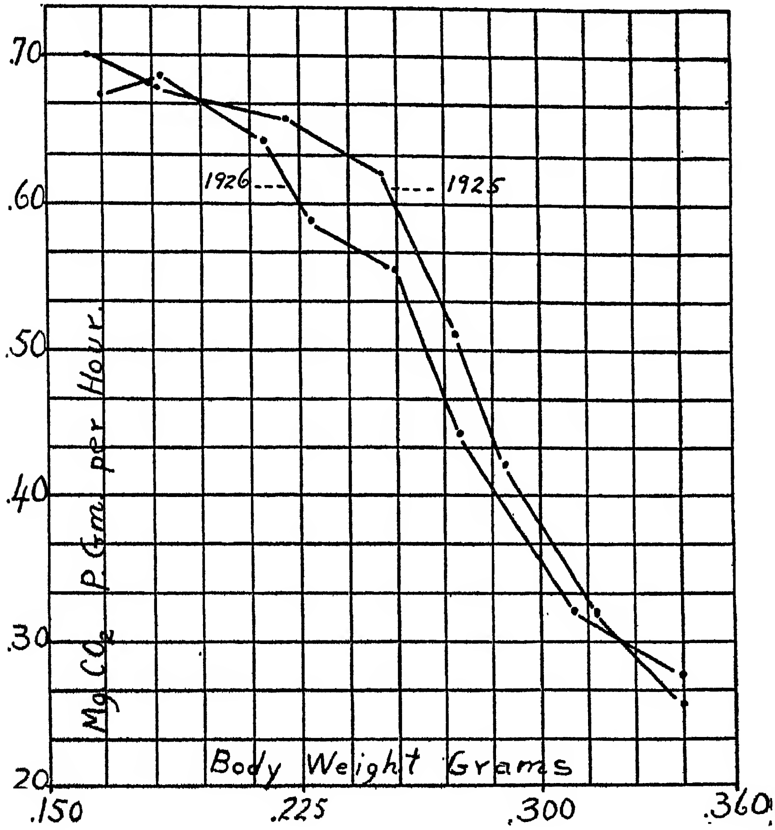


FIG. 1. RATE OF CO_2 OUTPUT OVER PERIOD OF THREE MONTHS

Time interval 10 days. Temperature 22°C. Abscissas, gram body weight per insect. Ordinates, milligrams CO_2 per gram insect per hour. For further explanation see description in text.

OBSERVATIONS

The carbon dioxide output of the nymphs under ordinary laboratory conditions was taken as representing the standard output, to which comparisons could be made with the data secured under experimental conditions. The determinations were made every ten days and the data taken over a period of three months. The animals were still in good condition at the end of this period. The results (fig. 1) show a relatively smooth curve; the rate of CO_2 output is higher for animals lighter in weight and decreases

progressively as the animals increase in body weight. Differences in body weight, especially in nymphs, are closely correlated with differences in age, and one is led to assume that younger individuals have the higher rate of respiratory output. Smaller animals are generally more active and are immature and growing.

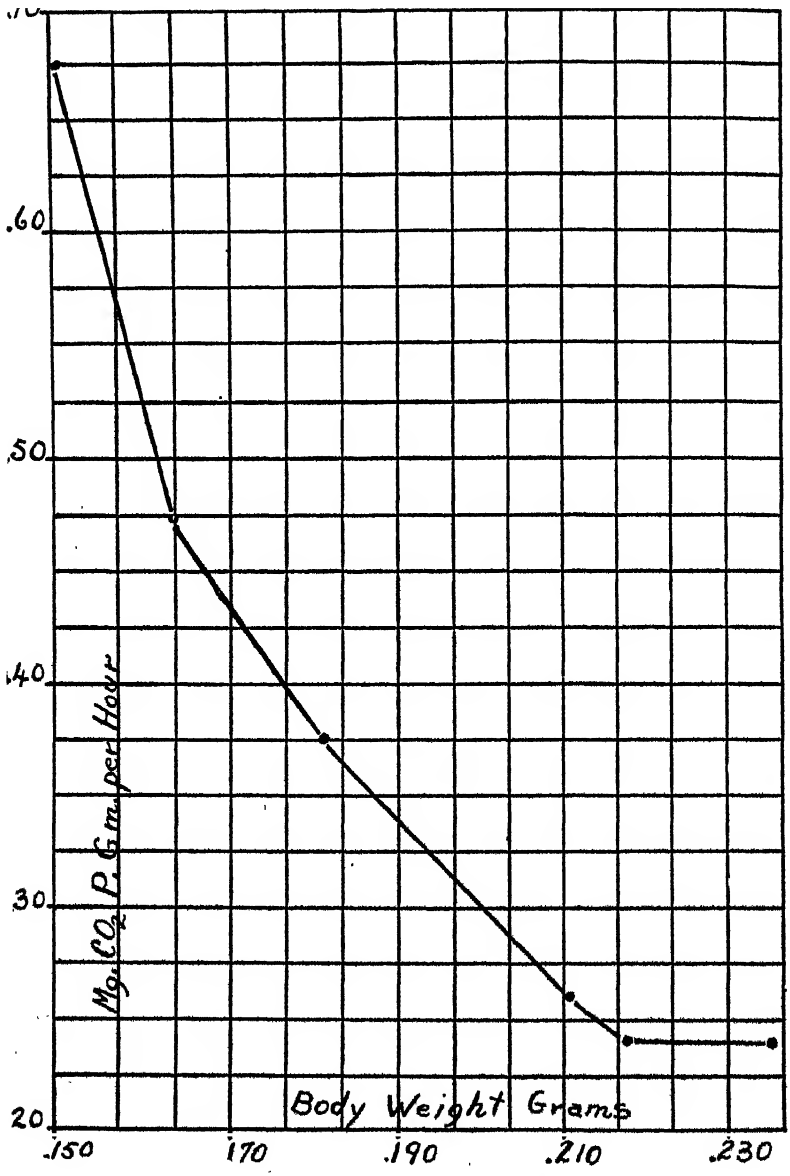


Fig. 2. Rate of CO_2 Output in Darkness

Time interval 7 days. Temperature 22°C. Abscissas, gram body weight per insect. Ordinates, milligrams CO_2 per gram insect per hour. For further explanation see description in text.

The starvation experiments were also carried on at 22°C., and the results showed that the carbon dioxide output decreased during the first week of starvation, but in each set of insects the output increased during the second week. The explanation of this increase is questionable. It may be that at this stage the nymph draws heavily on its reserve food or on its tissues. During the third and fourth weeks, the animals showed a steady decrease in metabolic rate. Nearly all the starved nymphs died before the seventh week, although two lived two months without food. In comparing the results of the starvation experiments with those of the controls, one could observe that the carbon dioxide output of a starving insect decreases in one week by an amountcomparable to the decrease in twenty days in a younger insect and to ten days in the older animals. At the end of four weeks of starvation, the carbon dioxide output was about the same as the output of the controls at the end of three months. It was interesting also to note an increase in weight in the starving insects. Since the nymphs are aquatic, this increase was probably due to the replacement of reserve fat by water during starvation.

The effect of darkness on carbon dioxide output is shown in figure 2. The metabolic rate decreased progressively with the weeks of darkness up to the sixth week, when four individuals died. Although the experiment was then brought to a close, the remaining nymphs were kept in the dark until all died, which occurred within a period of two weeks. That the metabolic rate of these animals is decreased by darkness can readily be seen by comparing the data here given with the data obtained from the controls. Per unit of weight the CO_2 output of the nymphs was much less than that of the control animals. A control insect weighing 0.214 grams gave off 0.6499 milligrams of CO_2 per hour, while an insect in darkness weighing 0.211 grams produced only 0.2345 milligrams.

Since most of the animals lived but six or seven weeks, the decreased CO_2 production must have been accompanied by a pathological condition resulting in early death. It is evident that light is necessary for the normal physiological processes, and that a lack of it produces an abnormal condition bringing about death. It would be interesting in further research to determine what part of the spectrum is of greatest importance in the normal life of these nymphs.

Figure 3 represents the average amounts of carbon dioxide given off by three sets of insects as the temperature of the water in which they were living was gradually raised. Most of the authors already cited determined the CO_2 output at each increase in temperature without making a study of the metabolic rate after a longer exposure to the same temperature. Instead of making the usual successive determinations at different temperatures, three determinations were made at each temperature. These records were made after twenty-four, forty-eight, and seventy-two hours exposure to the given temperature. In following this plan, a different curve was secured than is usually drawn. Reference to the graph shows that the CO_2 output goes up for each temperature after the twenty-four hours of exposure, but goes down again after the longer periods of exposure. The output is about normal after seventy-two hours at the given temperature. These results were found to be true in the case of each rise in temperature. If one connected with a line the twenty-four hour points on this graph, the usual rising curve could be secured. However, according to the method of determination followed

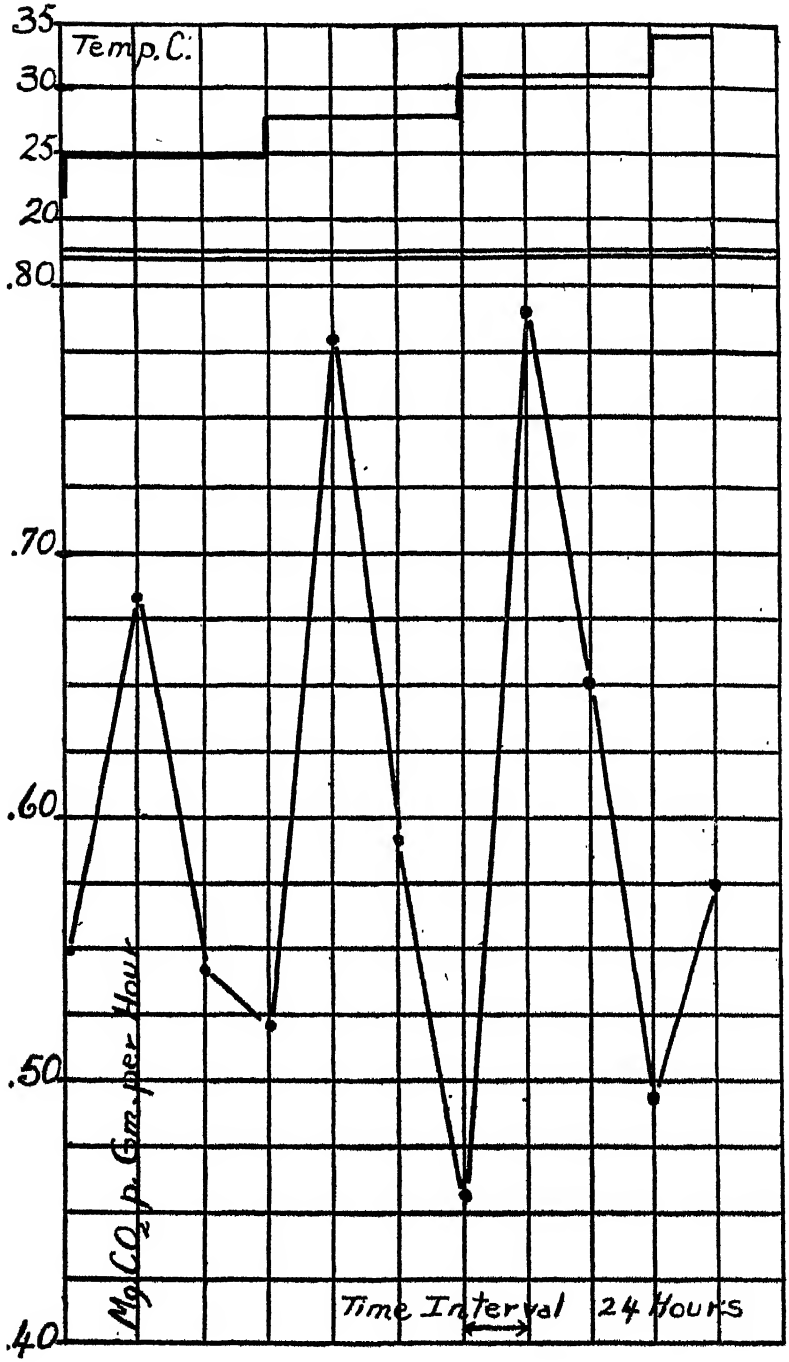


FIG. 3. RATE OF CO_2 OUTPUT AT HIGH TEMPERATURES

Abscissas, time in hours. Ordinates, at top, temperature in degrees Centigrade; at bottom, milligrams CO_2 per gram body weight per hour. For further explanation see description in text.

here, the insects show a mechanism for adjustment or acclimatization as evidenced by their carbon dioxide output. Above 31° the temperature has a deleterious effect upon the organism, for the insects respond but slightly to a

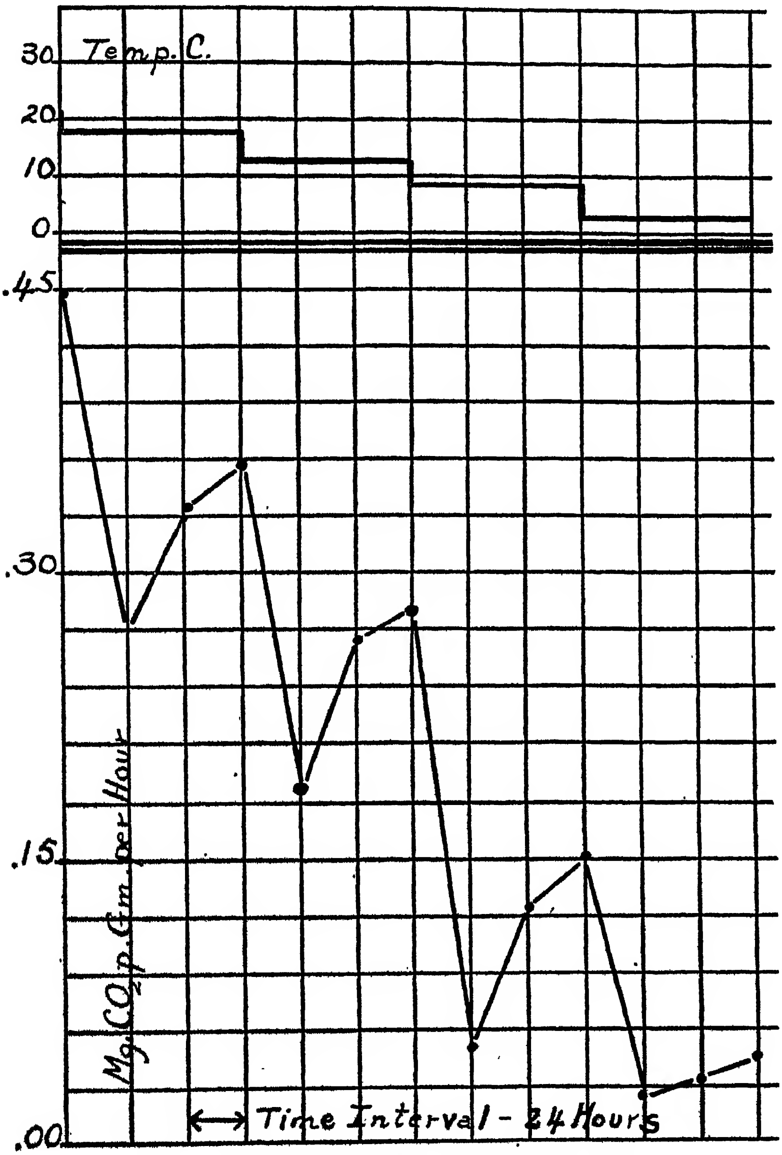


FIG. 4. RATE OF CO_2 OUTPUT AT LOW TEMPERATURES

Abscissas, time in hours. Ordinates, at top, temperature in degrees Centigrade; at bottom, milligrams CO_2 per gram body weight per hour. For further explanation see description in text.

The greatest output is between 28° and 31°C., this representing for the nymphs the maximum in catabolic reactions. further rise in temperature. At this high temperature the decreased carbon dioxide production is no doubt accompanied by

a physiological injury, for the animals died after twenty-four hours in water at 34°.

The insects used in the experiments to show the effect of low temperature on CO_2 output were somewhat larger than those used in the previous experiments. The former experiments were carried on in the fall months, while the present experiments were carried on in the winter, since it was thought advisable to use running water from the lake at a time when it maintained a constant temperature of 6°. Comparisons may be made, however, with insects of similar weight in the controls, to determine the relative amounts of carbon dioxide given off. The same scheme of duration of time at each temperature was used as previously employed in the records with rising temperature. Figure 4 shows that the carbon dioxide output decreased progressively with falling temperature after twenty-four hour durations, but also shows an acclimatization to a low temperature after being exposed to it for a longer period of time. The carbon dioxide output drops for each drop in temperature, but the output increases again in forty-eight and seventy-two hours at a given temperature. At 3°, the metabolic processes are going on at a very slow rate and acclimatization at this temperature was only slight. Low temperature did not affect the nymphs in any permanent way, for they lived a normal length of time after the experiment was completed.

The writer has attempted to review the field of metabolic experiments on insects and to point out the interesting work that has been done on this group of animals. There are many phases of the subject yet untouched and these offer tempting problems for further research.

LIST OF LITERATURE

(1) Allee, W. C., and Stein, E. R. 1918. Light reactions and metabolism in May-fly nymphs. Jour. Exp. Zool., 26: 423–458.

(2) Battelli, F., und Stern, L. 1913. Intensität des respiratorischen Gaswechsels der Insekten. Biochem. Zeitschr., 56: 50–58.

(3) Bodine, J. H. 1921. Factors influencing the water content and the rate of metabolism of certain Orthoptera. Jour. Exp. Zool., 32: 137–164.

(4) ———. 1923. Hibernation in Orthoptera. Jour. Exp. Zool., 37: 457–488.

(5) Bodine, J. H., and Orr, R. R. 1925. Respiratory metabolism. Biol. Bull., 48: 1–14.

(6) Brues, C. T. 1927. Animal life in hot springs. The Quart. Rev. Biol., 2: 181–203.

(7) Bütschli, O. 1874. Ein Beitrag zur Kenntnis der Stoffwechsels, insbesondere der Respiration bei den Insekten. Arch. f. Anat. u. Physiol., 348–361.

(8) Davenport, C. B. 1897. Experimental Morphology. New York. Vol. 1.

(9) Dirken, M. N. J. 1922. La relation entre les changements de température et la consommation d'oxygène par les animaux à sang froid. Archives Néerland. de Physiologie, 7: 126–131.

(10) Farkas, K. 1903. Über den Energieumsatz des Seidenspinners während der Entwicklung im Ei und während der Metamorphose. Pflüger's Arch. f. d. ges. Physiol., 98: 490–546.

(11) Fink, D. E. 1925. Metabolism during embryonic and metamorphic development of insects. Jour. Gen. Physiol., 7: 527–545.

(12) ———. 1925. Physiological studies on hibernation in the potato beetle. Biol. Bull., 49: 381–406.

(13) Krogh, A. 1914. On the rate of development and carbon dioxide production of chrysalids of *Tenebrio molitor* at different temperatures. Zeitschr. f. allg. Physiol., 16: 178–190.

(14) ———. 1916. The Respiratory Exchange of Animals and Man. London and New York.

(15) Loeb, J. 1888. Der Einfluss des Lichtes auf die Oxidationsvorgänge in thierischen Organismen. Pflüger's Archiv f. d. ges. Physiol., 42: 393–407.

(16) Loeb, J., and Northrop, J. H. 1917. On the influence of food and temperature upon the

duration of life. Jour. Biol. Chem., 32: 103–121.

(17) Luciani, L., et Lo Monaco, D. 1893. Sur les phénomènes respiratoires de la chrysalide du bombyx du murier. Arch. ital. de Biol., 19: 274–283.

(18) Luciani, L., et Piutti, A. 1888. Sur les phénomènes respiratoires des œufs du bombyx du murier. Arch. ital. de Biol., 9: 319–358.

(19) Newport, J. 1836. On the respiration of insects. Phil. Trans. Royal Soc. London, 529–566.

(20) Northrop, J. H. 1926. Carbon dioxide production and duration of life of Drosophila cultures. Jour. Gen. Physiol., 9: 319–324.

(21) Parhon, M. 1909. Les échanges nutritifs chez les abeilles pendant les quatre saisons. Ann. des Sc. natur. Zool., Ser. 9, 9: 1–58.

(22) Plateau, F. 1872. Recherches physico-chimiques sur les articules aquatiques. Bull. Acad. Roy. Sci. Belg., 34: 274–321.

(23) Regnault, V., et Reiset, J. 1849. Recherches chimiques sur la respiration des animaux des diverses classes. Annales de Chimie et de Physique, 26: 299–519.

(24) Roedel, H. 1886. Über das vitale Temperaturminimum wirbelloser Thiere. Zeitschr. f. Naturw., 59: 183–213.

(25) Sayle, M. H. 1928. Factors influencing the rate of metabolism of Aeshna umbrosa nymphs. Biol. Bull., 54: 212–230.

(26) Slowtzoff, B. 1909. Über den Gaswechsel der Insekten und dessen Beziehung zur Temperatur der Luft. Biochem. Zeitschr. 19: 497–503.

(27) Sorg. 1805. Disquisitio Physiologica circa Respirationem Insectorum et Vermium. Rudolstadt.

(28) Sosnowski. 1902. Contribution à l'étude de la physiologie du développement des mouches. Bull. intern. de l'Acad. des Sciences de Cracovie 568.

(29) Spallanzani, L. 1787. Opuscules de Physique, animale et végétale. Trans. Jean Senebier, 8: 56–58.

(30) ———. 1807. Sur la respiration des insects. Genève.

(31) Tangl, F. 1909. Beiträge zur Energetik der Ontogenese. 6, 7. Arch. ges. Physiol., 130, 1, 55.

(32) Treviranus, G. R. 1831. Versuche über das Atemholen der niederen Tiere. Zeitschr. f. Physiol. von Tiedmann und Treviranus, 4: 1–39.

(33) Vernon, H. M. 1897. The relation of the respiratory exchange of cold-blooded animals to temperature. Jour. Physiol., 21: 443–496.

(34) von Brücke, E. 1909. Der Gaswechsel der Schmetterlingspuppen. Arch. f. Physiol., 204.

(35) von Linden, G. 1912. Die Assimilationstätigkeit bei Schmetterlingspuppen. Leipzig.

(36) Weinland, E. 1905. Über die Stoffumsetzungen während der Metamorphose der Fleischfliege. Zeitschr. f. Biol., 47: 186–231.

SOCIAL PARASITISM IN BIRDS

By HERBERT FRIEDMANN
Department of Biology, Amherst College

IF ONE were to enumerate the main features characteristic of birds, the chances are that the habit of nest-building would be among the first to be mentioned. This indicates in no uncertain fashion the universality of this habit in this large group of vertebrates, and in turn, this very universality immediately focuses our attention on those relatively few species that neither build nests nor care for their eggs or young. These birds lay their eggs in occupied nests of other species, to whose care they are left, and because of this habit are, for want of a better term, said to be parasitic. The habit is not true parasitism in the real biological sense, and may be called social or breeding parasitism. Few problems in the study of animal behavior have aroused more interest for a longer period of time, and from Aristotle to the present time there is an unbroken series of attempts to explain the origin of this peculiar habit. In the early days of biological science this question was limited to a single species, the well known European cuckoo, *Cuculus canorus*, and it was of this bird that Aristotle wrote, ending his discourse with the cautious sentence, "People say that they have been eye-witnesses of these things." Since his time a great many individuals have also claimed to have been eye-witnesses of these and similar things, but it is only within the last century that accuracy and precision have been brought into play in these observations and the facts separated from the interpretations. Less than two centuries ago it was found that many cuckoos in Asia were also parasitic, but the habit was still supposed to be confined to the one family of birds.

In the early days of the last century it was discovered that the cuckoos were not the only birds with parasitic breeding habits, and that the cowbird of North America, *Molothrus ater*, a bird belonging to an entirely different order, also exhibited this remarkable mode of reproduction. Later, workers in southern South America found that some of the neotropical cowbirds were likewise parasitic, and observers in Africa announced that the habit was also found in some of the honey-guides. Quite recently a few of the African weaverbirds were shown to be parasitic, and just a few years ago a South American duck, *Heteronetta atricapilla*, was found to possess this habit as well. At present, this manner of reproduction is known to occur in five widely separated and distantly related families of birds: the cuckoos (*Cuculidae*), the hangnests (*Icteridae*), to which group the cowbirds belong, the weaverbirds (*Ploceidae*), the honey-guides (*Indicatoridae*), and the ducks (*Anatidae*). Of the cuckoos about seventy species are known to be parasitic; of the hangnests, only the cowbirds and the rice grackle, half a dozen species in all; of the weavers, only three; of the honey-guides, all the species of whose breeding habits we have any knowledge, less than half a dozen; and of the ducks, a single species. The entire number of parasitic species forms but a

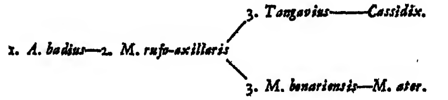
mere handful out of the thousands of kinds of birds known to science.

As the number of birds known to be parasitic increased, interest in the subject increased accordingly, and an enormous literature grew up around the problem. The number of theories brought forth to account for the origin of the habit became almost as great as the number of writers on the subject. Before adding still another to the long list of theories, we may at this point examine the evidence and material available. In order to make the problem more approachable we may limit it for the present to one group of birds,—the cowbirds.

THE COWBIRDS

The term cowbirds as used in this paper includes the true cowbirds (genera *Agelaioides*, *Molothrus*, and *Tangavius*) and the rice grackle (*Cassidix*). The latter is in reality nothing but a large edition of *Tangavius*, although it is not generally called a cowbird. The genus *Agelaioides*, restricted to Argentina, Paraguay, Uruguay, and Brazil, is the oldest and most primitive of the cowbirds. It contains two closely related species, *A. badius* of Argentina, Paraguay, and Uruguay, and *A. fringillarius*, a pale representative form in eastern Brazil. The former is the one that is now well known and will be called the Bay-winged Cowbird in this paper. The genus *Molothrus* contains the most typical cowbirds;—three species with many races; —*M. rufo-axillaris* of Argentina, Uruguay and Paraguay; *M. bonariensis* of South America from Patagonia to Panama; and *M. ater* of North America, from the highlands of central Mexico to the region of Lake Athabaska, and from the Atlantic to the Pacific. *M. rufo-axillaris* will be referred to as the Screaming Cowbird, *M. bonariensis* as the Shiny Cowbird, and *M. ater* as the North American Cowbird. The genus *Tangavius* contains one species known in life and one known only from four skins preserved in the American Museum of Natural History in New York and the Königliche Museum für Naturkunde in Berlin. The former species is *T. aeneus*, the Red-eyed Cowbird, the latter is *T. armenti*, Arment's Cowbird.

Before taking up the reproductive habits of the different species it is necessary to form a mental picture of their phylogenetic relationships, so that we shall be able to fit the habits into the genealogical tree of the group. There is not space available here to present all the evidence, of which there are several independent lines; a mere diagrammatic outline will have to suffice. The evidence is given fully in my book *The Cowbirds* now being published by Charles C. Thomas of Springfield, Illinois, by whose permission some quotations are made in this article.



This scheme of relationship is supported by geographical (distributional) data, as well as by various lines of biological data such as coloration, song, migration, and courtship display.

BREEDING HABITS OF THE COWBIRDS

The Bay-winged Cowbird is in every way the most primitive species of the group and probably represents the original condition of the ancestral cowbird stock. It is non-migratory, and is strictly monogamous. It winters in flocks, and early in spring the individuals leave the flock in pairs. There is no courtship display of any sort. The pairs then wander about looking for old or empty nests, but frequently fight with other birds for possession of occupied nests, usually with the result that the

bay-wings succeed in ousting the builders and usurp the nests, throwing out any eggs or young that may happen to be present. The birds then breed in these nests, taking care of their eggs and young as do ordinary birds. If no old or occupied nests are available the birds build for themselves and construct very creditable nests, indicating that they still possess the nest-building instinct but bring it into action only as a last resource, when all other means fail them. However, even when (as in most cases) they take over old nests, they do a certain amount of nest-building:—repairing or adding to the lining, enlarging the entrance in the case of domed nests, rearranging small twigs on the outside, etc. Then, after the nests are renovated or completed, as the case may be, the females lay their eggs, usually five in number, and begin incubating, and rear their young as do most normal nesting kinds of birds.

The Screaming Cowbird is apparently a direct evolutionary offspring of the bay-winged stock. In the adult stage the plumages of the two species are very different, but the young (juvenal) birds are exactly alike, both having the coloration of the Bay-winged Cowbird. Like the Bay-wing, the Screaming Cowbird is non-migratory. It is, if anything, even more strictly monogamous, as it is found in pairs all year round, even in the middle of the Argentine winter. So closely are the members of each pair united to each other that it is quite the exception to see a single individual at any time. On a few occasions I have found single birds or groups of three, but in an overwhelming majority of the cases the birds were in twos. Like the Bay-winged Cowbird, it is a very late breeder—the season for eggs being from December to the end of February for these two species, whereas most small birds in Argentina breed from September to January—and the geographical and ecological ranges of the two species are entirely coincident. The eggs and young of the two are practically identical, but the eggs can be told apart with considerable certainty by one who has studied them intently. The Screaming Cowbird is, however, parasitic in its breeding habits and confines its parasitic attentions to one species—the Bay-winged Cowbird.

It is interesting to note, in passing, the ironical aspect of this situation. As far as the available evidence indicates, the main factor coincident with the late breeding of the Bay-winged Cowbird is the abundance and availability of nests built and since deserted by other species. In other words, there seems to be some correlation between the apparent dislike for nest-building on the part of the Bay-wing, and its late breeding season. By breeding late it avoids the task of building. The Screaming Cowbird also is a late breeder but is parasitic, and inasmuch as no other birds are breeding so late in the season, the Bay-wing automatically becomes the chief, if not the only, victim. In this way additional work devolves upon the species that originally adopted a late laying season to avoid work.

The Shiny Cowbird is a far more widely ranging species than either of the two already mentioned, and occurs from Patagonia to southern Darien (Panama), while the Bay-wing and the Screaming Cowbirds are found only in the northern part of Argentina, Uruguay, southern Brazil, Paraguay, and Bolivia. It is migratory in the southern part of its range and is less monogamous than either of the other two species found in South America. In general it tends toward monogamy, but in localities where it is very numerous its sexual relations seem unable to maintain themselves unchanged in the face of the pressure of population numbers and the

birds become more or less promiscuous, or possibly polyandrous, in their mating habits. This species (and also the Screaming Cowbird) has a very different type of courtship display and song, differing in this respect from the most primitive species of the group. The Shiny Cowbird presents a new feature, that of a differential sex-ratio, the males being much in excess of the females, while in the first two species the sexes are about equal in numbers. This excess of males almost seems a result of the parasitic habit, as it allows for a numerical increase of the species without too great an increase in egg producing individuals. If too many eggs were produced too few of the natural foster-parents would be able to bring up any of their own young and thereby provide an adequate supply of victims for the succeeding seasons. The numerical status of the parasite depends very largely on those of the common host species. It has been shown that in the cowbirds (18) there seems to be a definite correlation between the sex-ratio and testicular size asymmetry. To quote from that paper:

> The condition in—(the cowbirds)—is interesting and suggestive. Two of them, *Agelaioides badius* and *Molothrus rufo-axillaris*, have no sexual dimorphism in plumage, are monogamous, and ratio of the sexes is even, one male to one female. These two species have the testes equal in size. The other three, *Molothrus bonariensis*, *Molothrus ater*, and *Tangavius aeneus*, have sexual dimorphism in plumage, are more or less promiscuous with a tendency towards polyandry, and the males in all three outnumber the females by at least three to two, or by not less than fifty per cent. In these three species the left testis is much larger than the right. It is interesting to note that of the five the first two (with equal testes in breeding adult males) are the most primitive species of cowbirds in all respects. *Agelaioides badius* is more or less normal in its reproductive habits, but all the others are parasitic . . . . The development of this habit allowed for an increase of males in proportion to females as true mating and pairing were probably of less importance to parasitic species than to one tied down by nesting and parental obligations. The parasitic habit is simplest in *Molothrus rufo-axillaris* and this species still pairs off in its ancestral monogamous fashion . . . .

The Shiny Cowbird is an early breeding species, and is parasitic on a great variety of small birds; in fact almost all the small birds breeding in the range of this cowbird are probably parasitized. Over eighty species have been found caring for its eggs or young.

The North American Cowbird is very similar in its habits to the Shiny Cowbird. In song, courtship display, relative number of the sexes, sexual relations and lack of specificity of host species, the two are very similar. However, the Shiny Cowbird has the parasitic habit less well developed and wastes large quantities of its eggs, either by laying them on the ground and leaving them there or by laying too many eggs in one nest or in deserted nests, etc. The North American bird is more efficient in the disposition of its eggs, and wastes relatively very few of them. About two hundred species of small birds are known to be parasitized by this cowbird.

The Red-eyed Cowbird represents another branch of the cowbird tree and is more similar to the Screaming Cowbird than to any other. It is parasitic on several species, usually birds of genera fairly closely related to itself, such as *Icterus*. The males somewhat outnumber the females, and in general the relations of the sexes are similar to the condition in the North American Cowbird.

THE BREEDING AREA

One other topic demands our attention before we can piece together the various bits of evidence offered by the different species of cowbirds. This is the matter of the individual breeding area or territory. Howard (32) has shown that normally each pair of birds establishes an individual

breeding area within the confines of which they tolerate no others of their own species. The size of the territory in most cases seems to depend on the abundance and availability of food for the young. As a rule (in by far the greatest number of instances) the males establish the territories and wait there for the arrival of the females. The females then choose the exact site of the nest within the territories of their respective mates. The establishment of the territory is primarily the business of the male, and his main task during the early part of the breeding season seems to be the defense and maintainance of the territory. The territory seems more fundamental than the nest in the complex of instincts of the male.

It follows that the sexual relations of the birds (i.e. monogamy *vs.* promiscuity, etc.) depend largely on their territorial relations, and inasmuch as these two are intimately bound up with the mode of reproduction, we may profitably examine the territorial situation in the cowbirds.

In the Bay-winged Cowbird the problem is somewhat simpler than in the others, as each pair has its nest and is thereby tied down to a definite area. However, instead of the usual procedure, we find the reverse is followed. The wintering flocks break up into pairs in the spring, and the pairs of birds go about looking, not for territories, but for nests. They will fight with the builders, if need be, to gain possession of the nest, or else will quietly occupy an uncontested one. Then the territory is extended radially around the nest, instead of the nest-site being chosen within the territory as in normal birds.

This altered conception of the breeding territory manifests itself in the defense of that territory. Instead of being the basic thing, the area becomes secondary to the nest and its defense is correspondingly weakened or lessened. This weakening of the defense opens an easy path to a distorted type of sexual relations, such as promiscuity or polyandry.

The territorial situation in the case of the next species, the Screaming Cowbird, is of interest in that it presents a rather unusual state of affairs, although superficially it seems quite ordinary. This species, as already noted, pairs off early in the season but does not begin to breed until nearly midsummer (January and February). Nevertheless, quite early in the spring it establishes its territories, often as early as the first week in October. Sometimes the period elapsing between the time of territorial establishment and the actual inception of egg-laying amounts to two or even nearly three months. Yet during all this time each pair maintains its particular sphere of influence. Pairs from adjacent territories do not join or mix promiscuously although they do sometimes form temporary groups of four to six birds in neutral feeding areas. Having no nests to care for or young to provide with food, why should these birds establish territories and stay in them day after day, sometimes for nearly a quarter of a year, without making any use of them? One would hardly expect a nonparasitic species endowed with strong, fully developed parental instincts to limit its individual liberty of action for so long a time merely in anticipation of, and preparation for, its reproductive activities. The Goldfinch of North America (*Astragalinus tristis*) breeds at the same relative season (reversed) as the Screaming Cowbird, but the flocks of the former do not break up for pairing and breeding purposes until about a month before egg-laying commences. Furthermore, not only do they have to establish territories and procure mates in this month but also to build nests, which the Screaming Cowbird

never does. The late breeding of the Goldfinch is doubtless an adaptation to seasonal food supply but in the Screaming Cowbird it seems an old habit phylogenetically derived from the ancestral stock, of which the Bay-winged species is the surviving member. Food supply cannot explain why the Bay-wing and the present species breed so late in the season, as the food of the young of both these birds is the same as that of the young Shiny Cowbird, which is an early breeding bird. However, the Bay-wing breeds late because it habitually breeds in old nests of woodhewers (*Anumbius* and *Synallaxis*) and ovenbirds (*Furnarius*). Late in the season there are plenty of these nests available, while earlier they are fewer in number, most are occupied by the builders and the Cowbirds would have to fight for them. The greater ease and certainty with which these nests could be obtained later in the season probably was largely responsible for the postponement of the breeding season in the Bay-winged Cowbird. The present bird, the Screaming Cowbird, shows in several ways that it is an offshoot from the Bay-wing stock, and its habit of breeding very late is doubtless due to a similar tardiness of reproductive season in the stock from which it evolved.

DESERTION OF BREEDING TERRITORIES

The late breeding coupled with fairly early establishment of "territories" which remain unused for a considerable length of time has brought about a very interesting condition in the Screaming Cowbird: namely, not infrequent desertion of territories before egg-laying commences, with the subsequent establishment of new territories later as the reproductive urge becomes more imminent. In this connection the following observations, taken from my book, are of interest.

In Concepción district, Tucumán, Argentina, I watched several pairs of Screaming Cowbirds whose territories were more or less adjacent. As the season wore on I found that one pair forsook its territory and disappeared. The male of this pair was identifiable by an extreme harshness in his notes. He and his mate were well nigh inseparable. I never saw either bird alone or more than a couple of feet away from the other, even when feeding on neutral ground. The desertion of this territory took place between the twenty-second and twenty-fourth of November. On December second I was surprised to find the same male securely established in a new territory about a mile away. With him constantly was a female, just as before. Whether or not it was the same female I could not say, but of the identity of the male I had no doubt. The old territory of this male was occupied by a new pair of birds four days after it was deserted by the first pair. From this it would hardly seem possible that the "fitness" of this territory had in some way been lessened to the extent of causing the original pair of tenants to desert it. It was possible that the female of the original pair had died and the male had deserted on that account. In order to test this I shot the females of three pairs on three nearby, and, to me, well known territories. In none of these cases did the males desert; they remained and soon found other mates. I can attribute this desertion to no cause other than the diminishing potency of the territorial instinct with the passing of time between the establishment and the utilization of the territory in question. Another bit of evidence in this connection was gathered at the height of the breeding season of the species (January) at Santa Elena in Entre Rios, eastern Argentina. I was studying a Bay-winged Cowbird's nest, making

daily notes of everything concerned with it. On January 8, 1924 I noted that a pair of Screaming Cowbirds flew into the tree in which the nest was and stayed around in the nearby branches but were kept away from the nest by the Bay-wings. Suddenly another pair of Screaming Cowbirds flew into the tree and joined the first pair. A minute later the second pair, (the newly arrived birds), flew over to the nest and were chased back by the Bay-wings. They flew back to the first pair and a little while later both pairs flew off together, screaming as they flew. It seemed that in this case one of the two pairs of Screaming Cowbirds was encroaching on a nest in the territory of the other. The birds being strictly monogamous, only one pair would occur in any one territory, and the other pair must have just recently come in. Screaming Cowbirds were not very plentiful in that district, and there was plenty of land available for the other pair to use. There were also plenty of Bay-wings scattered over the country. This looked as though the second pair had not yet established themselves in a breeding territory although it was very late in the season. It is hardly possible that this pair had not attempted to do so before; it seems likely that they were birds that had deserted a territory and were not yet settled in a new one.

POPULATION PRESSURE AS A MODIFIER OF BREEDING HABITS

In the case of the Shiny Cowbird, the numerical abundance of the species usually modifies or hides the true state of affairs. The sexual and territorial relations of this species are easily over-ridden by the pressure of population, resulting in undue competition for breeding areas. In this species the factors influencing the extent of the individual territories are not associated directly with the food supply, but with the abundance of nests in which to deposit the eggs. The denser the small bird population, the smaller the territory of each Cowbird. Where the Cowbirds are very abundant the territories as such become almost impossible of definition and demarkation. The results of a protracted study of this species indicate the following facts. In areas where the birds are not extremely abundant, they pair off regularly and each pair has its own territory. In places where the Cowbird population is great, the birds still pair off, but inasmuch as they make no pretense of protecting the territory other individuals filter in, remain there a day or so and then pass on. Consequently it is more usual to see several of these birds together (with the males predominating in number) than to see them in groups of two. The following observations, taken from my book, will illustrate this point. I watched a certain pair of Shiny Cowbirds, whose territory I knew, every day for several weeks. The female laid the first egg in a nest of a Chingolo Song Sparrow (*Brachyspiza capensis*) on October 25th.

I was surprised, however, to find that another female Cowbird also laid in this nest on the same date. It looked as though the male was constant in its territorial relations but that females came and went promiscuously. However, in the next few days I found that the same female had laid an egg in each of four chingolo nests in this territory, including nest no. 1. The eggs were laid at intervals of one day, but at the same time, each day I kept finding eggs of other female Cowbirds in nests where they certainly were not the day before. Thus in nest 1 no less than four different female Cowbirds deposited one egg each, two of them removing (or apparently removing) one of the eggs already in the nest. In nest no. 2, eggs were deposited by two different Cowbirds; nest no. 3 contained eggs of two different Cowbirds; nest no. 4 contained only 1 Cowbird egg. All in all I judged, by the size, color, marking and texture of the eggs as well as by the date of deposition that no less than six different females had deposited eggs in nests within the limits of this particular territory. However, the important point is that one bird, which I shall call

the real mate of the male whose territory is under discussion, laid an egg in each of the four nests, or 4 eggs in all, while of the other five females using these nests, four laid but one egg apiece and the other laid two. Furthermore the two eggs laid by the last bird were laid four days apart. This means either that this particular female wandered about from one territory to another or else that it laid during the interval in nests in this territory which I never found.

[In this connection I should advise any reader interested particularly in this subject to study the observations of Mr. E. P. Chance on the European Cuckoo, *Cuculus canorus*, and acquaint himself with his theory of a "dominant" female in each territory, an explanation with which my observations on *Molothrus* are in complete agreement, keeping in mind the sole difference that the Cowbirds lack specificity in their parasitism.]

Nevertheless, in spite of all this confusing data the total evidence leads me to believe that the Shiny Cowbird is chiefly monogamous and each mated female sticks to one territory but that both the sexual and territorial relations are so weak as to be very easily modified or sometimes even destroyed by conditions, particularly by the unnatural, increased density of cowbird population per given area around cultivated districts. Of course this frequently results in what seems to be sexual promiscuity and does destroy, in great measure, the "territory," in the sense that that particular area is no longer the domain of only one female but has become the happy hunting grounds of all that may care to make use of it. The same is largely true for the North American species, *M. ater*.

In fact Barrows (9), than whom no more reliable observer ever wrote on Argentine birds, said that he was inclined to think that *Molothrus bonariensis* differed less from *M. ater* in its habits than was generally supposed. "Its great abundance and the comparative openness of the country will in great measure account for the large number of eggs found as well as for the numbers sometimes observed in single nests . . . . Of course this overdoes the matter so as to compel the rightful owner to desert the nest, but I suspect that our own Cowbird would be no wiser under similar pressure."

One more point needs to be discussed here. The males outnumber the females to the same extent as they do in *M. ater* of North America,—about 3 males to every 2 females. Assuming that every breeding female has a mate and but one mate, there would be still one-third of the males without mates and consequently without any means of satisfying their sexual desires. If several males having no "territories" or "spheres of influence" joined in the pursuit of the same female, disaster to the race would undoubtedly ensue. But each male (except in the case of the yearling birds that begin breeding very late) has his own territory and there he awaits the coming of a mate. The greater the number of Cowbirds to a given area, the greater is the competition for territories with the result that the territories are smaller than elsewhere where the Cowbirds are fewer. The smaller each territory the less assurance a female has of a requisite number of nests in which to lay, and so what probably happens is this: After utilizing all the available nests in the territory of any one male she passes on to that of the next. If that territory is already occupied by a female, the newcomer finds the available nest supply inadequate and passes on still further afield. Often she may leave an egg or even two in a certain territory before passing on. Inasmuch as there are at least fifty per cent more males than females, it means that after each female has exhausted the "territory" of her particular male she still has half as much more coming to her in other places. This arrangement not only gives all the females a fairly equal chance to lay the maximum number of eggs but it also brings about a state of affairs wherein each male can find satisfaction in the appeasement of its sexual desire. However, this state of affairs can hardly be called polyandry for, although in the course of a season each female may have several mates, she has only one at a time and only one in a territory. Most monogamous birds change mates with each brood and yet no one would call the females polyandrous, the males polygamous or the species promiscuous. In the Cowbirds, if the birds were originally more than one brooded, the broods have been merged in adaptation to the parasitic habit. One would be more justified in calling the males polygamous as they have intercourse with some of the wandering females while still mated themselves. Yet the male does not leave his territory to collect a harem but takes what comes his way, and not having any concept of parental instinct can hardly be accused of polygamy. There is a great difference between this and a nonparasitic species wherein the male has a paternal interest in two nests simultaneously.

In fact if the females did not wander further afield after exhausting the possibilities of the territories of their respective mates, at least one-third of the males would not be able to appease their sexual desires without forsaking their territories and intruding into those of other males. The loyalty of each male to his territory is not to be thought of as "virtuous" in any way [For the biology of "virtue" see any of the

pseudo-scientific sentimental nature writers.], but is due to the fact that he would have nothing to gain by wandering.

So then, it seems that the Shiny Cowbird is monogamous, under normal conditions, but where artificial conditions have caused a great, unnatural increase of the species, the inherent instinct is not strong enough to stand unmodified against the increased competition, and frequently is modified so extensively as to belie its original status.

The sexual and territorial relations in the North American Cowbird are practically the same as in the preceding species, except that they are usually less violently modified, as the birds are not so crowded. In a general way this is also true of the Red-eyed Cowbird, but in the latter species the numbers are usually low enough so that the birds have sufficiently large territories to avoid competition, and monogamy is more easily observed. It is only fair to say that less is known of the habits of this species than of any of the others, but for our purposes it is relatively unimportant, as it is off the main line of Cowbird descent.

HOW DID THE PARASITIC HABIT COME ABOUT?

Before utilizing the above data in the formulation of an explanatory theory it may be well to present and comment on the leading current hypotheses. The first to be considered is that the source of the parasitic habit is to be sought in the polyandrous condition which all parasitic birds were supposed to exhibit. Pycraft (40) and Fulton (24) are among the best known exponents of this view. While it is possible (though not probable) that some parasitic cuckoos may be polyandrous, the cowbirds are certainly more or less monogamous, and such promiscuity as occurs is more likely to be a result than a cause of the parasitic habit. *Vidua macroura*, a parasitic African weaverbird, is also monogamous, and Chance (13) writes of the European cuckoo that " . . . . whether cuckoos are polygamous, polyandrous, or promiscuous is a very open question. I am inclined to the belief that they are, at least often, promiscuous. I should not, however, lightly dismiss the theory that some pair as normal birds. . . . ." Fulton admits that the question of polyandry and parasitism is all in a circle and that it is hard to say which came first. He inclines to the view that polyandry causes parasitism. In the cowbirds the circle is still open and there can be no question that parasitism is not caused by polyandry.

The best theory advanced as yet, and one which my studies tend to support in part, at least, is that of Professor F. H. Herrick. This writer studied the cyclical instincts of birds and found that not infrequently the cycle is interrupted by various causes which result in a general lack of harmony between its successive parts. He suggested that the parasitic habit may have originated from a lack of attunement of the egg-laying and the nest-building instincts which resulted in the eggs being ready for disposition before a nest was ready for them. His theory was based largely on a study of the Black-billed Cuckoo, *Coccyzus erythrophthalmus*, and a comparison of its life history with that of the European Cuckoo, *Cuculus canorus*, which, of course, is parasitic, while the former is not.

He found that of all the perturbations which are apt to arise at almost any step in the cyclical sequence of instincts the commonest was a failure in the "adjustment of nest-building to the time of egg-laying," and it was at this point that he suggested the parasitic habit took its rise.

"The door is thus opened wide to parasitism in its initial stage, whenever the acceleration of egg-laying or the retardation of the building instinct becomes common, with or without irregu-

larity in the egg-laying intervals." He applied this idea to both the Cuckoos and the Cowbirds and probably would have extended it to cover the parasitic Weavers and Honey-guides as well had he known of them at the time. He writes that "Parasitism could never succeed as a general practice on a large scale, and the fact that it is a specialty of two families of birds shows that it is probably correlated with a peculiarity which they possess in common. This is to be found in a change in the rhythms of the reproductive activities, leading to a change of instincts. . . . . As to the 'why of this problem', that is, why has the normal rhythm of the reproductive cycle been disturbed . . . . nothing is certainly known. . . . ." (Herrick, 30).

The first writer to see that one explanation would not serve for all the different groups of parasitic birds was G. M. Allen. In the chapter on parasitic birds in his admirable book (1) he discusses all the parasitic groups in a general way and ends by saying that one must be prepared to find that the parasitic habit has been acquired in more than one way, and independently in the different groups exhibiting this habit. Wisely refraining from offering an explanation of parasitism, he suggests several "possible ways of origin." One of the possibilities is that parasitism may have arisen from the occasional laying of eggs in strange nests by birds that are very sensitive to the ovarian stimulus provided by the sight of a nest with eggs resembling their own. This is substantiated by experimental evidence collected by Craig, who found that in doves ovulation could be induced by comparable stimuli. In the case of the Flicker [*Colaptes auratus*] ". . . . the presence of a nest-egg seems to encourage them to keep on laying as if to attain a number whose contact stimulus would satisfy the brooding instinct. It may be that in the case of those ducks whose eggs seem so often to be laid promiscuously in nests of their neighbors, the mere sight of a nest with eggs resembling their own may act as a stimulus inducing them to add to the number" (1). Chance's field observations on the European Cuckoo are more or less in accord with this idea as he believes that the sight of her victims building their nests acts as a stimulus to ovulation so that the female parasite has an egg ready to be laid five or six days later. This is also true of some of the Cowbirds.

However, I cannot agree with this suggestion as a possible origin of the parasitic habit unless it be accompanied or preceded by a marked reduction in the attachment of the bird to its own nest. Even if the sight of eggs in strange nests stimulated egg production in a bird that was not parasitic, its natural instincts would associate the resulting eggs with its own nest and the bird would probably lay them there, unless, as I said above, its attachment to its nest were greatly diminished. Then, too, after it has laid the proper number of eggs, "whose contact stimulus would satisfy" its brooding instinct, it would normally begin to incubate and stop laying. If its nest-attachment were sub-normal in strength, the bird might then wander about to some extent and, on receiving more visual stimuli might revert to egg-laying. However in such a case, its own eggs would have a lessened chance of survival.

Another possibility suggested is that if a bird got into the habit of breeding in old nests of other birds, it would be easy

> . . . . to imagine that the bird might not discriminate between a newly completed nest and one recently abandoned. The result would be that if the intruder laid in the new nest, its rightful owners would resent the intrusion and prevent the repetition

of the act, even though they had themselves to bring up the unwelcome addition. It is likely, too, that the greater abundance of new than of deserted nests would favor the frequency of such mistakes until the parasitic habit would have become established.

This suggestion seems well founded and possesses the virtue of being simple. However even in this case, the actual origin of the parasitic habit is not explained. A possible method of evolution of the parasitic habit is suggested but no indication is given as to why the birds, if repulsed at a new nest, do not continue nest-hunting until they find an unoccupied one. Furthermore, birds that breed in old nests of other species do not normally lay the first egg on the same day that they first occupy the nest, but usually the possession of a nest seems to provide the stimulus necessary for egg-production. From this it follows that if a bird of such breeding habits did try to occupy a new nest it would either be repulsed by the owners before it had a chance to lay, or by the time it did lay an egg, the owners would have forsaken the nest, leaving the new occupant to care for its eggs, just as if it had originally gone to an old nest to breed.

In order to explain the origin of the parasitic habit we must first decide whether it is the result of a change from a normal nesting habit or whether it is a phylogenetically original one. All the evidence derived from a study not only of the cowbirds, but of birds in general, points unmistakably to the conclusion that parasitism is an acquired habit and not an original one. It is inconceivable to think of a long line of parasitic birds having no origin in normal nesting types. Again, for the evidence behind this statement I must refer the reader to my book as space does not permit of its inclusion here. It seems entirely safe and justifiable, then, to assume that parasitism was not the original condition in the cowbird stock. The problem, then, is not whether the cowbirds were or were not always parasitic, but how they lost their original habits and acquired their present ones.

LOSS OF PROTECTING INSTINCTS AS A FACTOR IN THE ORIGIN OF PARASITISM

To quote again from my book:

We have seen that all five species of Cowbirds establish breeding territories and that the distinctness or the definiteness of the territory is most pronounced in the most primitive, non-parasitic, Bay-wing, while it is least definite, and at times, almost imaginary, in the Shiny Cowbird and the North American *Molothrus*. In the Bay-Wing, and its off-shoot, the Screaming Cowbird, the birds are practically always strictly monogamous and only one pair is to be found in a given territory. In the other two species, where the parasitic habits are better developed, the territories are distinct chiefly in districts where the species are not abnormally numerous; but where they are unnaturally abundant, the territorial instincts are not strong enough to stand unmodified against the pressure of Cowbird population. Distinctness of territory depends on the amount of what may be called "territorial protection" displayed by the male. In most birds the male establishes a breeding territory and protects it from the inroads of other males of its own species. The female sometimes has this instinct as well. In the parasitic Cowbirds we see that the birds have still retained the territorial desire but have lost most of the instinct to protect their breeding areas. The original factor involved in this loss is the reversal of the usual method of territorial acquisition in the most primitive of the Cowbirds. We have seen that birds, usually the males, establish their territories, and then choose a nesting site somewhere within that territory. The Bay-winged Cowbirds however, reverse this process. They leave the winter flocks in pairs and, instead of staking out their "claims" they look for old or even new nests in which to breed. They fight for these nests if necessary, and when once in occupation, they extend the territory radially around the nest. In this way the territory, instead of being the primary consideration, becomes a matter of only secondary importance and with this reduction of its significance, the instinct to defend it is correspondingly lessened. In this way the amount of "territorial protection" displayed by the male is decreased and in the more recent, parasitic species, where the

protecting instincts are further reduced, the territory of any one male is very apt to be invaded by other males of its own species.

Furthermore, in the Bay-winged Cowbird, we have seen that the female has lost most of her protecting instinct and seems to spend most of what she has before laying her eggs, after which the eggs are largely dependent on the male for protection. The female is always quite bold and fearless when away from the nest, but very shy and nervous when incubating. Apparently she has the instinct to conceal her eggs in a nest, usually not of her own building, but has very little desire to protect them once they are laid. If not for the protection of the male, (and very fearless he is) she would probably be unable to care for her eggs, and if the male should lose his protecting instinct the result would be that the female would have the instinct to lay (or conceal) her eggs in nests but not to care for them (or protect them). This would open an easy path to parasitism. If we re-examine the habits and instincts of the other Cowbirds we find that this is exactly what has happened. The males have lost their protecting instincts and we find that the loss is more complete in *M. ater* and *M. bonariensis* than in *M. rufo-axillaris*. The very fact that we still find these somewhat obscure, but yet real, stages in the loss of the protecting instincts, only serves to emphasize the downward path these instincts have taken. So then, it may be said that the immediate cause of the origin of the parasitic habit in the Cowbirds was the loss of the protecting instinct of the male. The fact that the female, still earlier in the history of the group, lost most of her protecting instincts cannot be called a causative factor because as long as the male retained his instincts of defense, as in the Bay-winged Cowbird today, the birds were not parasitic. What caused the almost complete loss of these instincts in the male we cannot definitely say, but the factor which started the weakening, and finally brought about their destruction was the reversal of the territorial and nesting habits. When the territory became of only secondary importance the impulse to protect it was correspondingly weakened. At the risk of seeming paradoxical it might almost be said that the fact that the ancestral Cowbirds cared more about the nest than the territory had much to do with the origin of the parasitic habit. The complex of reproductive instincts became unbalanced and eventually collapsed. In other words, the birds were more interested in a secondary than a primary consideration with the result that the former suffered much more than the latter.

Fortunately we have a clue to the way in which the male lost his protecting instinct. In order to fully appreciate its significance it is necessary to digress for a moment and consider the evolution of the Screaming Cowbird from the Bay-wing stock. As already indicated in a previous section the Screaming Cowbird is obviously a direct offshoot of the stock of which the Bay-winged Cowbird is the living example. The range of the Screaming Cowbird is wholly contained within that of the Bay-wing and in general the habitat or type of country occupied by the two species is the same. I always found both species in the same type of environment. It seems then that there could have been no geographical or ecological isolation in this case to preserve and differentiate the budding form which in its present state we call the Screaming Cowbird. Consequently the isolation necessary to preserve the distinctness of the newly arisen species must have been physiological. The physiological isolation was probably that of differential breeding seasons. Probably the original *rufo-axillaris* was an early breeding bird (*badius* is a later breeder). Although *rufo-axillaris* today is a late breeder, the facts that its courtship season comes early in the spring, and that it establishes its territories very early, point to the conclusion that it once was an early breeding bird as *bonariensis* and *ater* are today. Inasmuch as the Bay-wing is nonparasitic and inasmuch as the Screaming Cowbird is a direct offshoot of this stock it seems probable that originally the latter species was also non-parasitic. In other words the change between the normal and the parasitic mode of reproduction occurred within the racial history of *M. rufo-axillaris*. Assuming that in most ways the original habits of the Screaming Cowbird were similar to those of the Bay-wing we should expect that the birds tried to breed in nests of ovenbirds, woodhewers, etc., but tried to do so early in the season. As elsewhere indicated the struggle for nests is much greater early in the season than later on, and the Screaming Cowbird, handicapped hereditarily by a weakened territorial instinct, probably could not succeed in this struggle. We have seen that sometimes Screaming Cowbirds establish territories in the spring, occupy them for considerable periods, and then desert them without ever having utilized them. This indicates very strongly that the weakened territorial instinct of the male is often insufficient to maintain its influence long enough to "make connections" with the somewhat more vernal development of the egg-laying instincts of the female. In this lack of attunement between the territorial instincts of the male and the egg-laying instincts of the female the parasitic habit probably had its origin. This lack of attunement seems to have been caused by the diminution of the protecting territorial instincts of the male and this diminution seems in turn to have been started by the reversal of the territorial and nest-building instincts in the stock from which the Screaming Cowbird evolved.

So much, then, for the cowbirds. In the other groups of parasitic birds, other factors seem to have been instrumental in bringing about the parasitic breeding habit. Too little is definitely known of their biology to attempt an explanation, but probably the habit arose differently in each of the five families containing parasitic species.

HOST SPECIFICITY IN THE CUCKOOS

In the cuckoos, we have one clue which indicates that territory had little to do with the inception of parasitism. This is furnished by the peculiar feature of host specificity shown by some of the species, especially in Europe and Asia, but to a lesser extent in Africa and Australia as well. In the classic case of the European Cuckoo, *Cuculus canorus canorus*, it is now well established that generally each female deposits all her eggs in nests of a single species. That is, one cuckoo may parasitize only meadow-pipits, another may lay its eggs only in nests of hedge-sparrows, while still another may victimize reed-warblers exclusively. Each individual has its own particular species of victim to which it generally limits its attention. The species *Cuculus canorus canorus* lays its eggs in the nests of a great number of different kinds of birds, but each individual tends to use the nest of but one kind. The parasitic habit in *Cuculus canorus canorus* may therefore be said to be characterized by *individual* host-specificity. In the Indo-Malayan region there are a great many genera and species of parasitic cuckoos, some of which have carried this specificity to an extreme with the result that the great majority, if not all, of the eggs are laid in nests of a single species or group of allied species. Thus the Indian Koel, *Eudynamis honorata*, lays its eggs wholly in nests of crows and jays. In British India it victimizes the Indian Crow, *Corvus splendens*, and the Jungle Crow, *Corvus macrorhynchus;* in Burma it foists its eggs upon the Burmese Crow, *Corvus insolens*, and the Burmese Jay, *Pica sericea;* in southern China the victim is another Jay, *Graculipica nigricollis*. In large districts in its range practically all the individual koels victimize the same species of bird. In other words, within each of these districts the individual host-specificity of each individual koel is the same as that of every other one, and taking into consideration the entire range of the species the number of host species is so small and the species so closely related that the individual host-specificities of all the koels are very similar. The parasitic habit in *Eudynamis honorata* may therefore be said to be characterized by *specific* host-specificity.

The development of specific from individual host-specificity may readily be accounted for by natural selection operating under conditions which would tend to emphasize the value of small differences. Thus, in the case of *Eudynamis honorata* the bird (and its egg) is too large to be successful with small fosterers. The crows are everywhere common and their nests open and plainly visible and the birds (and their eggs) fairly close in size to the koels. An abundant, accessible group of species being everywhere available, the individual koels having crows as their individually specific hosts would rapidly increase and gradually eliminate their less successful fellows that depended on more precarious and more uncertain specific hosts. In time the entire membership of the species *Eudynamis honorata* would be composed of individuals parasitic on crows.

During the course of my field work in Africa I found that the various parasitic cuckoos were ecologically isolated from each other to a very considerable extent, i.e., one species lived in dense forest, an-

other in open country, and among species of different genera living in the same type of country, one species restricted its parasitism to open, arboreal nests, while others laid only in domed nests either in low trees, or on the ground. The ecological factors affecting the ranges and habitats of the various parasitic cuckoos necessarily limit the number of host-species available to each species of cuckoo. In the tropics the number of species and of individual birds is very large and the resulting struggle for existence more intense than in the more lenient regions to the north and south. As a result of the keenness of the competition we find that similarity in habits survives side by side where those habits do not affect the same species. That is, a habit such as the parasitic one could survive far more easily in many species in the same region if they did not conflict with each other than if all were parasitic on the same group of host-species. So then, in the bushveldt of Africa we find that the little golden cuckoos, *Lampromorpha*, victimize weaver-birds, grass-warblers, and a few other types of birds, chiefly limiting their attention to the weavers and *Cisticolas*. Most, (almost all) of their victims build domed or covered nests, some of them on the ground. In the same districts we find that the crested cuckoos, *Clamator*, confine their visitations to open, arboreal nests, such as the golden cuckoos never molest. However, with a fair number of species to choose from there is no environmental reason why a certain individual parasite should further limit its range of activities by tending towards extreme host-specificity. It is not of any particular obvious benefit to the parasite to be still further restricted in this way.

The only way to arrive at a proper understanding of the way in which host-specificities might have begun is to study individual birds as well as species. In working on the reproductive habits of birds one of the first things to be determined is the extent and definiteness of the individual breeding territories. Chance and others have done this for the European Cuckoo, *Cuculus canorus canorus*, with splendid results. In the case of the African species of parasitic cuckoos I found that all of them establish definite breeding territories to which they adhere during the egg laying season. The males of some species, such as *Lampromorpha caprius*, *Chrysococcyx cupreus*, and *Cuculus solitarius*, are very faithful to their territories. The breeding territory in the case of a parasitic bird is based not upon a sufficiency of food for the young but upon an adequacy of nests for the eggs. As stated above the small golden cuckoos parasitize weaver-birds (*Ploceus*, *Hyphantornis*, *Otyphantes*, etc.) very frequently. A great many species of these weavers are arboreal and build their nests in large colonies, often as many as a hundred or more nests in a single tree. I found that in several cases a pair of didric cuckoos, *Lampromorpha caprius*, had established their territories around trees containing colonies of weavers and in at least four cases the territories were entirely restricted to single trees. These weaver colonies very seldom contain more than a single species of weaver, at least in my experience. In such cases the individual cuckoos, by restricting their territories to single trees, automatically limit their parasitism to single species. These weaver colonies are very common all over the African continent south of the Sahara and the didric cuckoos are also common and widespread. Therefore it seems very likely that individual host specificities are being formed in many individual cuckoos in the way just mentioned. It is impossible to imagine any cuckoo as originally

going around the countryside, inspecting various kinds of nests, making notes of the dietetics of the different species, and then repairing to its favorite perch to cogitate upon its researches and finally decide to limit itself to any one of them. Specificities must have originated without premeditation and survived because they were convenient. The fact that not all parasitic cuckoos are specific indicates that some never went through any such experience as the didric cuckoo is subject to. Host-specificity is decidedly convenient to a didric cuckoo fortunate enough to have within its territory a whole colony of suitable nests. Their territorial instincts of defense, like those of most parasitic species, are faulty and if they had to wander far afield in their search for nests the chances are they would not be able to keep any territory for themselves. That is what seems to have taken place in the Indian Koel, *Eudynamis honorata*. In this species individual territories as such seem non-existent any more. Baker (5) writes that the koel, ". . . . sets all Cuckoo laws in defiance; many birds breed in the same area and even in the same tree; and as many as eleven have been taken together."

The important point in all this for our immediate purpose is that the development of host specificities seems to depend on the strict adherence to individual breeding areas. This indicates that with the development of the parasitic habit in the cuckoos there was no coincidental diminution of the reality of the territory such as we find in the cowbirds.

The evolution of the habit in different groups of birds in widely separated parts of the world is one of the most notable examples of parallel development in the great group of birds.

LIST OF LITERATURE

(1) Allen, Glover M. 1925. Birds and Their Attributes. pp. 198–216.

(2) Audubon, John James. 1842. Birds of America, iv, pp. 18–22.

(3) Baker, E. C. Stuart. 1907. The oölogy of Indian parasitic cuckoos, pts. 1, 2, 3. Journ. Bombay Nat. Hist. Soc., xvii, pp. 72–83, 351–374, 678–696.

(4) ———. 1913. The evolution of adaptation in parasitic cuckoos' eggs. Ibis, 10th series, vol. i, no. 3, pp. 384–398.

(5) ———. 1922. Cuckoos; some theories about the birds and their eggs. Bull. Brit. Orn. Cl., cclxvii, vol. xlii, pp. 93–112.

(6) ———. 1923. Cuckoos' eggs and evolution. Proc. Zool. Soc. Lond., no. xix, pp. 277–295.

(7) Baldamus, E. 1853. Neue Beiträge zur Fortpflanzungsgeschichte des europaischen Kuckuks. Naumania, iii, p. 307.

(8) Barrett, C. L. 1906. The origin and development of the parasitical habits in Cuculidae. Emu, vi, pp. 55–60.

(9) Barrows, W. B. 1883. Birds of the lower Uruguay. Bull. Nut. Orn. Cl., viii, pp. 133–134.

(10) Bendire, Charles E. 1893. The cowbirds. Rep. U. S. Nat. Museum, pp. 587–624.

(11) Chance, Edgar P. 1916. Observations on the cuckoo. Brit. Birds, xii, no. 8, pp. 182–184.

(12) ———. 1919. Observations on the cuckoo. Brit. Birds, xiii, no. 4, pp. 90–95.

(13) ———. 1922. The Cuckoo's Secret.

(14) Coues, Elliott. 1874. Birds of the Northwest: a handbook of the ornithology of the region drained by the Missouri River and its tributaries. Dept. of the Interior, U. S. Geol. Surv. Terr. Misc. Publ. no. 3, pp. 164, 180–186.

(15) Craig, W. 1913. The stimulus and the inhibition of ovulation in birds and mammals. Journ. Animal Behavior, iii, no. 3, pp. 215–221.

(16) Evans, A. H. 1922. Notes on the life history of Cuculus canorus, with exhibition of eggs, Proc. Zool. Soc. Lond., pt. 1, pp. 197–199.

(17) Friedmann, Herbert. 1925. Notes on the birds observed in the lower Rio Grande valley of Texas during May 1924. Auk, xlii, no. 4, pp. 537–554.

(18) ———. 1927. Testicular asymmetry and sex

ratio in birds. Biol. Bull., lii, no. 3, pp. 197–207.

(19) Friedmann, Herbert. 1927. Notes on some Argentine birds. Bull. Mus. Comp. Zool., lxviii, no. 4, pp. 220–227.

(20) ———. 1927. A revision of the classification of the cowbirds. Auk, xliv, no. 4, pp. 495–507.

(21) ———. 1927. A case of apparently adaptive acceleration of embryonic growth rate in birds. Biol. Bull., liii, no. 5, pp. 343–345.

(22) ———. 1928. The origin of host specificity in the parasitic habit in the Cuculidae. Auk, xlv, no. 1, pp. 33–38.

(23) ———. The Cowbirds: A Contribution to the Study of Parasitism in Birds. C. C. Thomas Co., Springfield, Ill. (in press.)

(24) Fulton, Robert. 1903. The kohoperoa or koekoea, long-tailed cuckoo, (Urodynamis taitensis): an account of its habits, etc., etc. Trans. N. Zealand Inst., xxxvi, pp. 113–148.

(25) Gloger, C. W. L. 1854. Das geschlechtliche Erhaltniss bei den nicht selbst brutenden Vögeln. Journ. f. Ornith., ii, pp. 137–143.

(26) Grinnell, Joseph. 1909. A new cowbird of the genus *Molothrus*, with a note on the probable genetic relationship of the North American forms. Univ. Calif. Pub. Zool., 5, pp. 275–281.

(27) Herrick, Francis Hobart. 1907. Analysis of cyclical instincts of birds. Science, xxv, p. 725.

(28) ———. 1907. The blending and overlap of instincts. Science, xxv, p. 781.

(29) ———. 1910. Instinct and intelligence in birds. Pop. Sci. Monthly, pp. 532–558, 82–97, 122–141.

(30) ———. 1910. Life and behavior of the cuckoo. Journ. Exp. Zool., ix, pp. 171–233.

(31) ———. 1911. Nests and nest-building in birds. Journ. Animal Behavior, i, pp. 159–162, 244–277, 336–373.

(32) Howard, H. Elliott. 1920. Territory in Bird Life.

(33) Hudson, William Henry. 1920. Birds of La Plata, vol. i, pp. 69–115.

(34) Jourdain, F. C. R. 1925. A study of parasitism in the cuckoo. Proc. Zool. Soc. London, pp. 639–667.

(35) Leverkühn, Paul. 1891. Fremde Eier im Nest, Ein Beitrag zur Biologie der Vögel. pp. 1–4.

(36) Loeb, Jacques. 1918. Forced Movements, Tropisms, and Animal Conduct. Chap. xviii, pp. 156–164.

(37) Meikeljohn, R. F. 1917. Some Reflections on the Breeding Habits of the Cuckoo (*Cuculus canorus*). Ibis, 10th series, vol. v, pp. 186–223.

(38) Miller, Leo. 1917. Field Notes on Molothrus. Bull. Am. Mus. Nat. Hist., 1917, pp. 579–592.

(39) Pearl, Raymond. 1914. Studies on the physiology of reproduction in the domestic fowl. VIII. Data regarding the brooding instinct in its relation to egg production. Journ. Animal Behavior, iv, pp. 266–289.

(40) Pycraft, W. P. 1910. A History of Birds, pp. 127–134.

(41) Ridgway, Robert. 1902. The birds of North and Middle America, pt. 2. Bull. 50, U. S. Nat. Mus., pp. 202–212.

(42) Roberts, Austin. 1913. Egg-collecting in the Bushveld. Journ. S. Af. Orn. Union, ix, pp. 34–37.

(43) ———. 1917. Parasitism amongst finches. Annals Transvaal Mus., v, pt. 4. pp. 259–262.

(44) Sternberg, Chrysanthus. 1869. Zur Fortpflanzungsgeschichte des Viehstaares Molothrus sericeus. Journ. f. Ornith., xvii, pp. 125–136.

(45) Swynnerton, C. F. M. 1918. Rejections by birds of eggs unlike their own with remarks on some of the cuckoo problems. Ibis, 10th series, vol. vi, pp. 127–154.

(46) Thomson, J. Arthur. 1923. The Biology of Birds, pp. 309–310.

(47) Wallace, Alfred Russel. 1868. A theory of bird's nests. Journ. of Travel and Nat. Hist., p. 73.

(48) Watson, John B. 1909. The behavior of noddy and sooty terns. Pub. 103 Carnegie Inst. of Wash., p. 223.

(49) Wetmore, Alexander. 1926. Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. Bull. 133 U. S. Nat. Mus., pp. 383–388.

(50) Wilson, Alexander. 1810. American Ornithology, vol. 2, pp. 145–150.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

MAN RISES TO PARNASSUS. *Critical Epochs in the Prehistory of Man.*
By Henry Fairfield Osborn.
Princeton University Press
$3.00 *Princeton, N. J.*
6 x 8⅞; xix + 251

This volume comprises six lectures delivered to the students of Princeton University on the Louis Clark Vanuxem Foundation by the distinguished paleontologist of the American Museum of Natural History. A sequel to the author's well known "Men of the Old Stone Age," it reflects very largely his personal experiences in the research of man's prehistory.

The evidence for the great antiquity of man is reviewed and the record is carried back to Tertiary times in East Anglia, where flints of the Foxhall and rostro-carinate type are now credited to Pliocene man. The discovery of these artifacts by Reid Moir (in 1909) opened a new epoch in prehistory, for it divulged the existence of a fire and tool employing man much more ancient than indicated by any previously known evidence. Following, in the chronological order favored by Osborn, the successive precursors in the evolution of *Homo sapiens* are considered, the story of their discovery and subsequent study, their geological relations, and especially their mode of existence and cultural achievements. The treatment, one hastens to say, is not that of a dry physical manual. It is livened by personal anecdotes of the author's archeological adventures and its viewpoint is exceptional. In contradistinction to other writers who direct their main attention to the anatomical characters of fossil man, this author seeks to discern the evidence for the rise of his mind and spirit. To some thinkers evolution has brought a sense of something approaching the triviality of man. They see him as one among many in a struggle for existence, his survival the result of fortuitous circumstance, his ultimate destiny dependent on the vagaries of nature. For Osborn, on the contrary, the evidence is everywhere of his essential uniqueness and sublimity. His earliest achievements show him far removed from anything bestial, and the author is vigorous in his disapproval of what he calls the myth of our ape-ancestry.

Even *Pithecanthropus* is no lowly crea-

ture. Subjected to modern intelligence tests by the professor of psychiatry in Columbia University, it was determined—such power have intelligence tests—that he thought as a man, and probably spoke as a man, though with limited vocabulary. During the long period of time that has elapsed since the extinction of this type, man has moved steadily upward in the development of spirit. That, indeed, is the moral of Evolution. And if we heed the teachings of eugenics, his continued progress is assured, *i.e.*, "if our understanding of the spiritual, intellectual, as well as physical values of races becomes more widespread." Thus will he rise to Parnassus.

The book is generously illustrated, and contains a bibliography and an index.

STRENGTH OF RELIGION AS SHOWN BY SCIENCE. *Facilitating also Harmony Within, and Unity Among, Various Faiths.*
By Charles E. deM. Sajous.
F. A. Davis Co.
$2.50 5 x $7\frac{1}{2}$; 252 *Philadelphia*

This book is another attempt at reconciliation. We cannot say that it has converted us; the author's religion and his science seem to us about equally dubious. His cosmogony includes a God, as "a primary, coördinative, and dominating intelligence" (p. 132), and the ether, which is "autonomous or self-acting, and is thus independent functionally of God after having been bestowed by him upon nature at large" (p. 139). The ether is a somewhat unruly agent, and is apt to misbehave, to the damage of humanity; this, however, is not God's fault, and it is "both wrong and unjust" to blame Him for earthquakes and volcanoes. Besides, it is a man's own fault if he goes to live in a volcanic country; there are plenty of other safer spots (pp. 140–145).

As regards evolution, the author holds that living forms are descended from primordial one-celled ancestors, through a process of evolution, but that each living form has an entirely separate ancestry. In the case of animals, the original ancestors were created by the ether; in the case of man, there was apparently a special act of God, who planted a soul in the original germ-cell (Ch. VI).

The author holds that the fundamentals of religion, as expounded by him, must be taught in the public schools if the rising tide of immorality is not to overwhelm us.

CONCERNING MAN'S ORIGIN. *Being the Presidential Address given at the Meeting of the British Association held in Leeds on August 31, 1927, together with recent Essays on Darwinian Subjects.*
By Sir Arthur Keith. *G. P. Putnam's Sons*
$2.00 $5\frac{1}{2}$ x $8\frac{1}{4}$; xi + 188 *New York*

A collection of some of Sir Arthur's essays on Darwinism. The first three chapters contain his famous Presidential Address before the British Association delivered in August, 1927, that came as a challenge to Bryanism. In it is reviewed the support given to evolution by the paleontological discoveries made since Darwin's day. Following are a lecture about Darwin's life at Down, and several on various aspects of evolution permeated with the notion that it implies progress.

There is nothing profound in the book, and not a little that is dubious, *e.g.*, "The rage for cross-word puzzles is but one of the modern symptoms of our hunger for intellectual exercises." But it is never dull.

The treatment is not comprehensive

enough to warrant an index and there is none.

LAMARCK ET L'INTERPRÉTATION DE LA NATURE. *L'Histoire de la Nature Vivante d'après l'Œuvre des Grands Naturalistes Français. IV.*
By Louis Roule. *Ernest Flammarion*
12 francs net *Paris*
$4\frac{5}{8} \times 7\frac{3}{8}$; 247 (paper)

The first 150 pages of this book give an account of Lamarck's life and work; the remainder is an attempt to create a Lamarckian philosophy of nature. This part of the book, we are obliged to say, leaves us as unconvinced as does most other philosophy. The biographical chapters are interesting; they suffer, however, from patriotism.

GENETICS

ERBLICHKEITSFORSCHUNG AN PFLANZEN.
By Friedrich Oehlkers. *Theodor Steinkopff*
13 marks (paper) *Dresden*
14.50 marks (bound)
$6 \times 8\frac{3}{4}$; viii + 203

This is a review of the progress of plant genetics during the last fifteen years, constituting Vol. 18 of the series *Wissenschaftliche Forschungsberichte*. The discussion is confined in the main to general problems, with only such introduction of details as is necessary to illustrate the points. The material is treated under two main heads, hybridization and mutation, with the bulk of the space going to the former.

HANDBUCH DER VERERBUNGSWISSENSCHAFT. *Band II, Lieferung 4.* Containing following articles: *Das Inzuchtproblem*, by H. Federley, and *Selbststerilität, Heterostylie*, by E. Lehmann.
Gebrüder Borntraeger
5.80 marks $7 \times 10\frac{1}{4}$; 43 (paper) *Berlin*

The first numbers of this important *Handbuch* of genetics were reviewed at length in the last number of The Quarterly Review of Biology. The present section deals with the problem of inbreeding (Federley) and self-sterility and heterostyly (Lehmann). The high standard of the earlier parts is well maintained in these. Both papers carry extensive bibliographies.

EINFÜHRUNG IN DIE VERERBUNGSWISSENSCHAFT. *Ein Lehrbuch in Einundzwanzig Vorlesungen.*
By Richard Goldschmidt. *Julius Springer*
30 marks (paper) *Berlin*
32.40 marks (bound)
6×9; ix + 568

The fifth enlarged and improved edition of the author's well known textbook of genetics. A good deal of new material has been added in the text, and 68 new illustrations. The book is one of the best introductory texts in existence and in its revised form will continue its past success.

PALUDINENSTUDIEN ZUR FRAGE DER REZENTEN PALUDINA DILUVIANA. *Bibliotheca Genetica Band XI.*
By V. Franz. *Gebrüder Borntraeger*
20 marks 7×10; 144 (paper) *Leipzig*

An interesting general biological, biometric, and ecological study of the genus *Paludina*, with special reference to its evolution. *Paludina diluviana* is held to belong to the relatively thermophile southeast European *pyramidalis* group of the genus and to have no living descendants north of the Alps.

KONSTITUTIONSSEROLOGIE UND BLUTGRUPPENFORSCHUNG.
By Ludwig Hirszfeld. *Julius Springer*
18 marks $6\frac{3}{4} \times 10\frac{1}{4}$; 235 (paper) *Berlin*

A very useful work for all geneticists. It critically and in sufficient detail reviews all the work that has been done on blood groups. The thoroughness of the survey is indicated by the fact that the bibliography covers 26 pages of fine print. We heartily recommend this book to our readers.

SELECTIVE FERTILIZATION.
By Donald F. Jones.
University of Chicago Press
\$2.00 $5 \times 7\frac{3}{8}$; xii + 163 *Chicago*

An excellent review of the literature on selective fertilization and assortative mating, to which the author himself has notably contributed.

GENERAL BIOLOGY

FOIBLES OF INSECTS AND MEN.
By William M. Wheeler.
Alfred A. Knopf, Inc.
\$6.00 *New York*
$6\frac{1}{4} \times 9\frac{1}{4}$; xxvi + 217 + xi

Anything that Professor Wheeler writes is a delight, from every point of view. In this beautifully made volume he has collected together some of his addresses and essays on subjects of broad, general appeal. Here is preserved for all time the *Termitodoxa* address, a piece of satire which ranks with the very best in the English language. To find its peer one must go back to Swift. For professional reasons the biologist will be glad to have here in accurate form the essay on "The Ant Colony as an Organism," first published far in advance of its time, in the sense that biological thought had not then reached a level to appreciate the fundamental significance of this piece of work. The "Physiognomy of Insects," first published in The Quarterly Review of Biology, finds in this volume a permanent home. The Introduction to the volume is a masterly discussion of "autistic" or wishful thinking as contrasted with realistic or scientific thinking.

> Savages, children, theologians and many philosophers are inveterately addicted to autistic thinking and when, as commonly happens, this is compounded with the grand foible of verbalism, we get those astonishing aberrations of mythomania, superstition and metaphysics from which the race has been suffering ever since it began to think. Autistic thinking is essentially magical and fails utterly to attain its aim, which is a control, without a knowledge, of phenomena; scientific thinking, however, has shown that it can secure both a knowledge and a control of phenomena and that the latter cannot be secured without the former. In other words, experience has demonstrated that the explanations reached as a result of emotional thinking—i.e., thinking hobbled by fear, desire, aspiration, exaltation, etc.—are intellectually and in practice nugatory, sterile, misleading or even harmful, while those resulting from scientific thinking, though it has been seriously tried for only three centuries and by a very small fragment of the race, have proved to be fruitful beyond our wildest expectations.

Full of erudition without pedantry, pointed with wit, humor, satire, and irony, written with literary distinction and charm of the first order, this is such a book as but rarely is given to us poorer mortals.

STRUCTURE AND DEVELOPMENT OF THE "LIVING MATTER."
By F. Vejdovský.
Royal Bohemian Society of Sciences
\$35.00 *Prague*
$8\frac{1}{4} \times 11\frac{3}{4}$; vii + 360 + 24 plates
(paper)

Professor Vejdovský is the *doyen* of Czechoslovak biology. This work may perhaps be regarded as his valedictory

though we hope not. It is, in its magnitude and in the lavishness of its production, a truly colossal piece of cytological research. The plates will gladden the hearts of those who sigh sentimentally for the good old days of the *Journal of Morphology*, when we had such lithographic plates as were plates!

The work was in the main ready for publication before the war. It only now appears. One result is that the later reading to bring it up to date is not well correlated with what has been done before. Somehow the whole book gives one the impression that the world's cytological knowledge and viewpoint have gone ahead faster than Prof. Vejdovský has. He has two pet theories, with neither of which are cytologists nowadays completely in accord. One is that the acrosome is derived from "nuclear liquid;" the other is that Golgi bodies are a "mitotic apparatus." In spite of all this the book represents an enormous amount of careful observing, and every cytologist will wish to have it in his library.

ON ROUS, LEUCOTIC AND ALLIED TUMORS IN THE FOWL. *A Study in Malignancy*.
By J. P. McGowan.
H. K. Lewis and Co., Ltd.
10 shillings net *London*
$5\frac{3}{8}$ x $8\frac{5}{8}$; vii + 99

The author holds that leucosis of fowls (not defined in the text, but apparently a designation for tumors consisting of cells in the leucocytic series) and the Rous tumor No. 1 are identical pathologic entities, both local manifestations of a disease of the reticulo-endothelial system. The evidence is predominantly histological, consisting in the identification by the author in sections from both conditions of cells belonging to the lineage of the hemopoietic system. An explanation, hypothesis out of whole cloth, as to the etiology of the tumors is presented.

Those acquainted with the controversial nature of all the work involving the microscopic identification of primitive blood cells will be dubious of the conclusiveness of this sort of scientific labor.

There is a discussion of melanomata in fowls, and a review of recent work on the etiology of tumors, but no index.

ANNALS OF THE PICKETT-THOMSON RESEARCH LABORATORY. *Vol. III (Containing a Historical Survey of Researches on the Streptococci).*
£2 2 s. ($10 in America)
Baillière, Tindall and Cox, London
Williams & Wilkins Co., Baltimore
$8\frac{1}{2}$ x 11; vi + 316 (paper)

These annals are issued irregularly. Each volume contains about three hundred pages of text, and a large number of plates comprising three hundred to four hundred microphotographs of bacteria. They are devoted mainly to bacteriology, protozoology, biochemistry, and to recording photographically the whole range of bacteria and protozoa.

This is the first of two volumes which together are to deal comprehensively with the *Streptococcus* groups in general, while the subsequent volume will consider the pathogenic varieties. There are chapters on staining, cultivation, cultural characteristics, biochemical reactions, virulence, immunity reactions and others, with special reference to the importance of differential media and microphotography as an aid to classification and identification. Fifty-seven illustrative plates are appended, and a bibliography and index are included.

EDUCATIONAL BIOLOGY.
By William H. Atwood and Elwood D. Heiss.
P. Blakiston's Son and Co.
$2.75 *Philadelphia*
$5\frac{7}{8}$ x $8\frac{3}{4}$; xi + 469

This is a textbook for use in normal schools and teachers' colleges. Some of the more important topics which are considered are: The properties of protoplasm; reproduction; the interrelation of plants and animals from the simplest to the most complex, adaptation; variation; the laws of heredity; possibilities and limitations of environmental factors in training; laws of learning; and such content as will give some appreciation of man's place in the animal kingdom. The book is well illustrated. Bibliographies follow each chapter. Lists of educational problems are given. A glossary completes the book.

DIE WICHTIGSTEN KRANKHEITEN DES KANINCHENS. *Mit besonderer Berücksichtigung der Infektions- und Invasionskrankheiten.*
By Oskar Seifried. *J. F. Bergmann*
15 marks *München*
$6\frac{7}{8}$ x $10\frac{1}{8}$; viii + 160 (paper)

This book will be found extremely useful by all laboratory workers using rabbits as material. It is thoroughly documented and brings together in convenient form all that is known regarding the pathology, in both its clinical and anatomical aspects, of this animal.

DIE GESCHLECHTSCHROMOSOMEN.
By Franz Schrader. *Gebrüder Borntraeger*
16 marks *Berlin*
7 x $10\frac{1}{2}$; iv + 194 (paper)

This thorough and comprehensive critical review of the present state of knowledge regarding the sex chromosomes forms the first number of a projected series under the general title *Zellen- und Befruchtungslehre in Einzeldarstellungen*, under the general editorship of Prof. P. Buchner of Breslau. While the title of the present volume is in German the text actually is in English. It is a first-rate piece of work, which will be very valuable as a reference source. There is a bibliography covering 18 pages.

A COURSE IN GENERAL BIOLOGY.
A Laboratory Manual.
By Henry S. Pratt. *Ginn and Co.*
$1.48 $5\frac{1}{2}$ x 8; xiii + 178 *Boston*

This is a laboratory manual for use in General Biology. It contains somewhat more material than any class could carry through, but in this way it offers a wider field for selection. There are classifications of both animal and plant kingdoms and a glossary.

INNERE SEKRETION. *Ihre Physiologie, Pathologie und Klinik.*
By Julius Bauer. *Julius Springer*
36 marks (paper) *Berlin*
39 marks (bound)
$6\frac{7}{8}$ x $10\frac{1}{8}$; vi + 479

The indefatigable Dr. Julius Bauer of Vienna, known for his work on the constitutional factor in disease, now assembles and discusses the literature of endocrinology. The book is a useful addition to the reference literature in the field.

HOLZNAHRUNG UND SYMBIOSE. *Vortrag Gehalten auf dem X. Internationalen Zoologentag zu Budapest am 8. September 1927.*
By Paul Buchner. *Julius Springer*
4.50 marks $5\frac{1}{2}$ x $8\frac{1}{2}$; 64 (paper) *Berlin*

An interesting lecture on the problem of bacterial symbiosis in the alimentary tract of organisms using wood as food. Relatively little space is given to the termites, and a great deal to the wood-boring beetles.

GEHEILTE KNOCHENBRÜCHE *bei wildlebenden und in Gefangenschaft gehaltenen Tieren.*
By E. Korschelt and Hermann Stock.
Gebrüder Borntraeger
24 marks (paper) *Berlin*
26.50 marks (bound)
$6\frac{1}{4}$ x 10; iv + 176

A detailed study of the healing of broken bones in wild animals. Its interest is, on the whole, rather highly special. The illustrations are numerous and excellent.

HUMAN BIOLOGY

PROCEEDINGS OF THE WORLD POPULATION CONFERENCE. *Held at the Salle Centrale, Geneva, August 29th to September 3rd, 1927.*
Edited by Mrs. Margaret Sanger.
American Birth Control League, Inc.
\$5.00 $5\frac{3}{4}$ x $8\frac{7}{8}$; 383 *New York*

The World Population Conference convened in Geneva from August 29 to Sept. 3, 1927. Its purpose was to bring together representative scientists from various parts of the world for a discussion of the problems of population, and to make provision for its further study and consideration. There has since been formed a permanent organization, the International Union for the Scientific Investigation of Population Problems.

The present volume gives the English text of all the papers prepared for the Geneva meeting, as well as the supplementary remarks and discussion which followed their presentation. The gathering included most of the world's eminent scientists actively interested in population. Of special interest to readers of this journal is the important rôle taken by biologists in what would have been considered until recently the exclusive concern of sociologists and economists.

Leading papers were delivered by Prof. Raymond Pearl, of the Johns Hopkins University; Prof. A. Niceforo, of the University of Naples; Prof. H. P. Fairchild, of New York University; Prof. E. M. East, of Harvard University; Prof. Jean Bourdon, of the Sorbonne; Dr. Rajani Kanta Das, of the International Labor Office; Prof. Corrado Gini, of the Statistical Institute at Rome; Prof. T. N. Carver, of Harvard University; Prof. A. M. Carr-Saunders, of the University of Liverpool; Prof. Lucien March, of the University of Paris; Prof. A. Grotjahn, of the University of Berlin; Prof. H. W. Methorst, of the International Statistical Institute, The Hague; Dr. Kark Arvid Edin, of the University of Stockholm; Dr. Julius Tandler, of the Public Health Department of Vienna; Dr. F. A. E. Crew, of Edinburgh University; Dr. Boleslav Rosinski, of Poland; M. Albert Thomas, of the International Labor Office; Dr. J. W. Gregory, of the University of Glasgow; Dr. A. Koulisher, of the University of Paris; Prof. Livio Livi, of the University of Rome; Prof. Charles H. Wickens, of the Commonwealth Bureau of Census and Statistics, at Melbourne; Mr. E. J. Lidbetter; Prof. H. Lundborg, of the State Institute for Race Biology at Uppsala; Dr. Warren S. Thompson of the Scripps Foundation, U. S. A.

We may presume that the authors summarized their current views on the more

significant phases of the population problem as seen from the viewpoint of their special knowledge. The report therefore constitutes a handbook of reference for the most expert opinion on important aspects of the population question. In view of the increasing pressure of the problem and the probable great importance of the International Union, it is likely to become historic.

There is an index and a "Who's Who" of the conference.

THE ARUNTA. *A Study of a Stone Age People. Vols. I and II.*
By Sir Baldwin Spencer and F. J. Gillen.
The Macmillan Co.
$14.50 $5\frac{3}{4} \times 8\frac{3}{4}$; liv + 646 *New York*

In these two impressive volumes, the authors, the second now deceased, continue their pioneer and exhaustive studies of the manners and morals of the Australian aborigines. The present work follows the investigations of the Central Australian tribes known as the Arunta, reported in their *Native Tribes of Central Australia*, published in 1899. In contradistinction to other explorers of these tribes, who obtained their information from natives who had come under the influence of civilized missionaries, the present writers were fully initiated members of the Arunta tribe, being considered to belong to the Bultara section and the Udnirringita or witchetty grub totem. From this indigenous vantage point they went over the ground of their previous studies and rewrote and amplified their first account.

After an introductory chapter, which gives a broad picture of the life of the people in their native surroundings, the succeeding ones take up, in great detail, their individual customs. Such typical chapter headings as "Social Organization," "The Totems," "Initiation Ceremonies," "The Achulpa Tradition," "Death, Burial and Mourning Ceremonies," "Method of Obtaining Wives" indicate the thoroughly descriptive character of the treatment.

Following the main work, there are a number of appendices which contain, among other subjects, the names of parts of the body, and a discussion of the supposed distinction of the aborigines into straight and wavy-haired individuals.

There are many photographic illustrations, a glossary of native terms used, and an index.

IN SEARCH OF OUR ANCESTORS. *An Attempt to Retrace Man's Origin and Development from Later Ages Back to Their Beginnings.*
By Mary E. Boyle. *Little, Brown and Co.*
$3.50 $5\frac{1}{2} \times 8\frac{1}{2}$; 287 *Boston*

The Abbé Henri Breuil, renowned archaeologist of France, suggested to the authoress that she reverse the usual procedure and tell the history of man starting at the later ages and tracing his development back to its beginnings. "Try to give a history of events which instead of sliding down the thread of the past should climb up it, going, as each one of us does, from the known to the less known, and at length to that region attained only by scientific investigation." The result was this book, and we regret to report that, judging by the effect on this reviewer, it is not happy. To proceed from the recent and better known to the remote and obscure seems an admirable formula for exploring history, but for recounting it the chronological order has become so habitual that its reverse seems awkward. When we read that the four divisions of the Tertiary Age are the Pliocene, Miocene, Oligocene and Eocene

there is an impulse to turn the book over, and we were prompted finally to read it like the translation of a Hebrew bible, beginning at the back. So read it is the tale of how man has developed from a primitive form of life in the "Primary Era" to the stage reached in *La Tène* III Period. This is a sizable history to compress into 270 pages, and since the author deals with paleontology and geology, as well as archeology, and does not neglect the history of these subjects themselves, it becomes in many places only a compact cataloging of facts. Withal, it is a fascinating story, the Etruscan and Cretan cultures being described with especial spirit.

There are many fine illustrations, some in color, and an index.

TRAVELS IN NORTH AFRICA.
By Nahum Slouschz.
The Jewish Publication Society of America
$2.50 *Philadelphia*
5 x 7⅝; x + 488

Nahum Slouschz is a peripatetic Hebrew scholar who has written widely on Jewish literature and ethnography. Here he recounts his observations among the *Haras* (the Arabic ghettos) of North Africa, which he explored in successive expeditions from 1906 to 1916. With a rare equipment of learning he discusses the physical setting, the historical background, the social and religious life of the communities he visited. The discursive style hinders somewhat the securing of an impression of broad perspective, but there are compensations in the colorfulness of the situations and incidents he recalls. There are, for instance, the cave dwellers of the Libyan hinterland who still maintain a *Talmud Torah* (Hebrew School), the desert Jews who on *Tish'a be Ab* (commemorating the destruction of the temple) emerge in the early morn to await the Messiah, who is to appear poor and mounted on an ass, (and therefore quite naturally mistake our author for him); the Jewish Croesus, who, a complete ignoramus himself, does not give a penny for the synagogue, but imports a poor talmudist from Egypt to marry his daughter; and much more of the curious and piquant.

A book that emphasizes the strangeness of this strange people.

There is no index.

THE NATIVE PROBLEM IN AFRICA. *2 vols.*
By Raymond L. Buell. *The Macmillan Co.*
$15 set *New York*
6¼ x 9½; Vol. I, xiii + 1045
Vol. II, x + 1101

How is an African native, who can easily satisfy his limited wants in his own fashion, to be persuaded to spend his time working for Europeans? That is the fundamental native problem in Africa. The attempts which have been made at a solution of this problem vary from outright slaving through all the degrees of peaceful persuasion and economic pressure. Dr. Buell has set forth these attempts in a scholarly, dispassionate manner, at some length, but never tiresomely. All things considered, the story is not one of which the Nordic need be proud.

The book contains a mass of information political, social, and economic. It is heavily documented; important reports and papers are printed as appendices to the various sections; the bibliography covers 66 pages and the index 50. It will be indispensable to anyone who wishes to learn about the present condition of the Negro in Africa. Incidentally, it may

be remarked that the concluding section, on Liberia, is of particular interest to Americans, in view of the Firestone rubber concession and its implications.

NEOPLASTIC DISEASES. *A treatise on Tumors.*
By James Ewing. *W. B. Saunders Co.*
$14.00 $6\frac{1}{4} \times 9\frac{1}{2}$; 1127 *Philadelphia*

A revised and enlarged edition, the third now, of the standard work of reference in English on neoplastic diseases. The classifications of mammary cancer and brain tumors have been altered, and the chapter on tumors of the bones entirely rewritten.

"The most substantial feature of the revision has been the interweaving of a great number of phrases, sentences, and paragraphs relating to matters of importance, both practical and theoretical."

The importance of illustrations is recognized and a considerable number have been added, but there is still room for improvement in their quality. The general biologist who wishes to get a sound idea of the present state of knowledge regarding cancer will find Ewing his best source.

MONGOLISM. *A study of the Physical and Mental Characteristics of Mongolian Imbeciles.*
By Kate Brousseau. Revised by H. G. Brainerd. *The Williams & Wilkins Co.*
$4.50 6 x 9; viii + 210 *Baltimore*

In this book the authors have brought together and examined all the known theories of Mongolism, a term used to denote a state of congenital mental deficiency whose marked physical characteristics are certain superficial resemblances to the Mongolian race. In addition they present their own material and information obtained from a questionnaire submitted to workers in various institutions for the feeble minded. From their data they draw the conclusion that most of the causes heretofore suggested for this condition must be discarded and suggest "that Mongolian imbecility is possibly induced by some obscure disturbance of the ductless glands." This book will be invaluable to the special worker in this field. A lengthy bibliography is appended.

THE EARLIER INHABITANTS OF LONDON.
By F. G. Parsons. *Cecil Palmer*
10 s. 6 d. $5\frac{1}{2} \times 8\frac{1}{2}$; 240 *London*

An historical and anthropological study of the various races that have lived in London, or before its existence, in the general location of the present city. Professor Parsons traces the mental and physical characteristics of these peoples from Paleolithic times through to the time of the Danish invaders, and in this way attempts to construct a picture of the early days of this city and of its former inhabitants. The book makes an interesting, as well as scientifically valuable, contribution to the literature of human biology.

THE STORY OF THE AMERICAN INDIAN.
By Paul Radin. *Boni and Liveright*
$5.00 $5\frac{3}{4} \times 8\frac{5}{8}$; xv + 371 *New York*

An interesting book, which gives in popular language and with good illustrations an account of what is known regarding the spread of the great civ-

ilizations that developed before white men discovered the Western Hemisphere, in Mexico, Central America and along the Pacific coast of South America from Ecuador to Peru. The author thinks it probable that there were "three invasions of North America, all of which started from Asia: an Australian, a Melanesian and a Mongolian proper. The Mongolians, coming last and in greatest numbers, overwhelmed the first two so completely that only in a few inaccessible regions of South America can traces of them still be detected. Everywhere else the Mongolian impress has been decisive. To all intents and purposes the American Indian is a Mongolian, physically, temperamentally and psychically."

A REPORT ON THE TREATMENT OF CANCER OF THE UTERUS AT THE SAMARITAN FREE HOSPITAL. *Reports on Public Health and Medical Subjects No. 47.*
By Janet E. Lane-Claypon and W. McK. H. McCullagh. His Majesty's Stationery Office
9 shillings *London*
$6 \times 9\frac{3}{4}$; iv + 36 (paper)

A study of the after-results of surgery for cancer of the uterus. The actual proportion of survivors in the Samaritan Free Hospital series, after abdominal hysterectomy, is given as 43.8 per cent alive after 5 years, and 36.6 per cent alive after 10 years. These figures are for cancer of the cervix only, and the percentage was taken upon all patients operated upon, excluding, however, those who died from causes other than cancer within the given period. For cancer of the body of the uterus, the corresponding proportions of survivors after operation are much higher—61.5 per cent (5 years). No death occurred after 5 years in the 10-year series.

THE KIWAI PAPUANS OF BRITISH NEW GUINEA. *A Nature-born Instance of Rousseau's Ideal Community.*
By Gunnar Landtman. The Macmillan Co.
\$12.00 $5\frac{3}{4} \times 8\frac{3}{4}$; xxxix + 485 *New York*

This book is a detailed account of the manners, customs, and beliefs of the natives of the western portion of British New Guinea, with whom the author lived for two years. It will be of interest to all students of anthropology and sociology. It is well and extensively illustrated. Our only serious objection is to the author's speaking of "pidgin-English" when he means "*bêche-de-mer.*" The confusion is common, but unjustified.

DIE RASSEN UND VÖLKER DER ERDE.
By Ernst Vatter. Quelle und Meyer
1.80 marks *Leipzig*
$4\frac{7}{8} \times 7\frac{1}{8}$; 134 + 14 plates

A little book in a series on *Wissenschaft und Bildung* designed to present the results of the labors of science to the populace, which has to read as it runs. In 131 small pages are covered *Rassenkunde und Völkerkunde und ihre historische Entwicklung, Rassenbegriff, Rassenentstehung und Rassen systematik, Rassenbeschreibung, die Sprache, Sprachgruppen und Völker.* The German love of detail does not escape even these popular presentations, as judged by this example.

LA PRÉHISTOIRE. (*Introduction aux études préhistoriques.*) *Les Ages de la Pierre. Les Métaux.*
By Raymond Furon. Albert Blanchard
20 francs $5\frac{1}{4} \times 8\frac{1}{2}$; 187 (paper) *Paris*

This is a brief outline of pre-history, intended for the intelligent layman. The author has succeeded in getting a great deal of information into a small space,

and without making his book dry reading. He has, as he explains in his introduction, confined himself to an exposition of facts, without any attempt at imaginative reconstruction of prehistoric life or mentality. The example might profitably be followed by other writers of science for the layman.

CONTEMPORARY SOCIOLOGICAL THEORIES.

By Pitirim Sorokin. *Harper and Brothers*
$4.00 $5\frac{1}{2} \times 8\frac{1}{2}$; xxiii + 785 *New York*

Professor Sorokin has here done a useful piece of work. He has classified all of the more important sociological theories that have existed for the last sixty or seventy years and has critically analyzed the fundamental principles underlying each. The book contains an enormous amount of data and has a large bibliography. The human biologist will find it a handy reference source, though he will probably not always agree with the author's position.

JEWISH COMMUNAL SURVEY OF GREATER NEW YORK. *First Section: Studies in the New York Jewish Population.*
Bureau of Jewish Social Research
50 cents 6 x 9; v + 45 (paper) *New York*

An interesting statistical survey of the Jewish population of Greater New York showing:—1. Movement of Jewish population in New York City. 2. Age distributions, births and deaths. 3. Causes of deaths among Jews. In 1925 there were 1,750,000 Jews in New York City, and the number increased 16.4 per cent between 1916 and 1925. In both years they made up about 30 per cent of the total population.

L'ETHNOLOGIE DU BENGALE.

By Biren Bonnerjea. *Paul Geuthner*
40 francs *Paris*
$7\frac{3}{8} \times 9\frac{3}{8}$; xxiii + 169 (paper)

The author of this book has, as he acknowledges, undertaken an almost impossible task. He has attempted to cover the entire subject of the ethnology of Bengal; and in consequence his book is nearly as difficult to read as a dictionary. This is not to say that he has written a bad book, but that his book is useful primarily for reference.

INTERNATIONAL HEALTH YEAR-BOOK 1927. *Reports on the Public Health Progress of Twenty-seven Countries in 1926.*
League of Nations
16 shillings; $4.00 (paper) *Geneva*
20 shillings; $5.00 (cloth)
$7\frac{1}{4} \times 9\frac{3}{4}$; 802

Summary reports for twenty-seven countries on the public health in 1926. The articles differ in length and somewhat in the material presented. Typical headings are Area, Population, Birth Rate, Mortality, Infant Mortality, Health Organization, Infectious Diseases.

Good brief statements, not in general detailed enough to tempt the reader to statistical research on the data given.

THE DEPENDENT AGED IN SAN FRANCISCO. *University of California Publications in Economics, Volume V, No. 1. Prepared under the Heller Committee for Research in Social Economics of the University of California.* *University of California Press*
$1.80 *Berkeley*
$7 \times 10\frac{3}{4}$; xiv + 127 (paper)

This is a study of the aged poor of San Francisco; it contains both statistical

material and case histories. The impression one gets is that the aged poor are in most respects probably not far from a random sample of the aged; but the material given does not allow one to form a definite judgment.

UNITED STATES CENSUS OF AGRICULTURE: 1925. *Reports for States, with Statistics for Counties and a Summary for the United States. Part I. The Northern States. Part II. The Southern States. Part III. The Western States.*
Issued by United States Department of Commerce, Bureau of the Census.
Government Printing Office
Washington
Part I, $1.75 $5\frac{3}{4}$ x 9; x + 1318
Part II, $1.75 $5\frac{3}{4}$ x 9; x + 1328
Part III, $1.00 $5\frac{3}{4}$ x 9; x + 512

These volumes constitute an invaluable reference source to the human biologist interested in the population problem. On this account we think it important to call attention to them here. They give, more completely than ever has been done before, the raw data as to how one large nation is fed.

THE MEDICAL DEPARTMENT OF THE UNITED STATES ARMY IN THE WORLD WAR. *Volume IX. Communicable and Other Diseases.*
Prepared under the direction of Maj. Gen. M. W. Ireland, by Lieut. Col. Joseph F. Siler.
U. S. Government Printing Office
$2.00 $6\frac{3}{4}$ x 10; 628 *Washington*

Excellent clinical, pathological, and statistical summaries of the army experiience with infectious disease during the war. No large amount of original data is given in a form to tempt further biometric analysis.

ZOOLOGY

LES LARVES ET NYMPHES DES DYTISCIDES, HYGROBIIDES ET HALIPLIDES. *Encyclopédie Entomologique X.*
By Henri Bertrand. *Paul Lechevalier*
100 francs *Paris*
$6\frac{1}{2}$ x 10; vi + 366 (paper)

At the present time there exist but two general works concerning the systematic study of the larvae of *Hydrocanthares.* Schiödte in his classical *De Metamorphosi Eleutheratorum* figured and described a few aquatic larvae belonging to the groups of Dytiscids, Hygrobiids and Haliplids (1865–1883), and much later, in 1901, Fr. Meimert published his *Larvae Dytiscidarum* treating only the larvae of the two first groups (to which he added the curious larvae of *Amphizoa* discovered by Hubbard in 1893) but already including about fifty forms. The author of the present work has endeavored to fill this gap in the literature by attempting a complete revision of all the known larvae and nymphae of the above mentioned families. The monograph is divided into four chapters. The first and more important one discusses larvae. The systematic study of the larvae of each family is preceded by a morphologic account stating the terminology that has been chosen, and designed to render the reading of the diagnoses easy. The different divisions from sub-families to genera and species are defined successively. For every genus, general generic characters are analyzed each in turn, and then those peculiar to every larval stage. As to species, every stage is the object of a diagnosis; then come particulars concerning the etiology, and the origin of the stock used. Dichotomous tables accompany this chapter; they have been devised for every known genus in the larval state, and for a great number of species of the Palaearctic region.

As to all the forms the examination of which could not be made, especially those of America, the material part of the information has been carried forward as an appendix.

The second chapter is devoted to nymphs. The material has been collected almost wholly by the author himself in various parts of France and reared. A few larvae, none of them yet described, belonging to the collections of the Museum in Paris, come from French colonies, chiefly Madagascar. In the course of the Systematic study, the first states of four genera: *Hydrovatus* Notsch, *Copelatus* Er., *Meladema* Cast, *Rhantaticus* Sharp, are described for the first time; thirty-three larvae and thirty-nine nymphae also have not been described before.

The third chapter gives a short account of the biology of the different families. The most original part relates to the habits of palaearctic forms and is based on the observations made while collecting or in the course of numerous breedings.

The fourth and last chapter collects the general results of the work; the relations between the systematic study of the first stages and that of the imagoes. Some curious examples of convergence are noted. Various suggestions are set forth concerning phylogenesis and adaptation, and also the meaning of the successive larval stages.

The illustrations are original and include about 200 drawings in the text, concerned with the general morphology and the features of the larvae and nymphae. There is also a series of thirty-three plates, comprising more than 300 drawings.

An excellent piece of systematic work.

BREHMS TIERLEBEN *in Einem Band.*
Revised by Georg Grimpe.
Bibliographisches Institut
25 marks 7 x 10; xxxvi + 836 *Leipzig*

For many years old Brehm has been the guide, philosopher and friend of the bright young biologist wholly immersed in physics, chemistry and mathematics, when he suspected that he might be called upon to display some knowledge about animals. Of course such a demand would never be made upon him in any modern up-to-date biological laboratory. But out in the cold world among roughnecks who did not understand that life is hydrogen ion concentration, electric potential, and differential equations, *et praeterea nihil*, a good deal of embarrassment has unquestionably been avoided by the judicious use of Brehm's *Tierleben*. Now the way is made still easier, for the juice has been pressed out of the big edition and put in one small-quarto bottle. The condensation has done no harm. It is still a good book.

THE BIOLOGY OF INSECTS.
By George H. Carpenter. *The Macmillan Co.*
$6.50 $5\frac{1}{2}$ x $8\frac{1}{2}$; xv + 473 *New York*

An interesting and instructive account of the biology of insects. The author states that he has described structural features only so far as seems necessary for the understanding of function and behavior; which indicates the bias of the book. We must say, however, that we suspect that the student will get a clearer idea of insect structure from this book than he might from many others. The book may be recommended to anyone who wishes a clear, simple, and authoritative account of how insects live. There is a sixteen page bibliography and a good index.

THE ORIGIN OF BIRDS.
By Gerhard Heilmann. *D. Appleton and Co.*
$7.50 6 x $9\frac{1}{2}$; vii + 210 *New York*

The author divides his book into

four parts. In Part I, some fossil birds are discussed; in Part II, the embryonic stages of birds and reptiles are compared; in Part III, some anatomical and biological features of both classes are given; in Part IV, an attempt is made to find the ancestor of birds and its relations. The book is written in an interesting style and is well illustrated, though just how Professor Heilmann arrived at the color of *Archaeopteryx* and *Hesperornis* is not revealed.

AN INTRODUCTION TO MEDICAL PROTOZOOLOGY. *With Chapters on the Spirochates and on Laboratory Methods.*

By Robert Knowles. Thacker, Spink and Co.

25 Rs. $7\frac{1}{4} \times 9\frac{5}{8}$; xii + 887 *Calcutta*

(Copies may be obtained from W. Thacker and Co., 2 Creed Lane, London, E. C. 4.)

This comprehensive treatise by the professor of protozoology in the Calcutta School of Tropical Medicine is divided into three parts. The first and largest consists of a series of 19 lectures on parasitic protozoa. The second part includes ten chapters on laboratory methods in medical protozoology. Finally there is a bibliography covering 92 pages, and a detailed index. The book is extensively and fairly well illustrated, and altogether constitutes a valuable contribution to the textbook literature in its field.

TIGERS, GOLD, AND WITCH-DOCTORS.

By Bassett Digby. Harcourt, Brace and Co.

$3.00 $5\frac{7}{8} \times 8\frac{3}{4}$; 341 *New York*

An entertaining volume of travels and experiences in Siberia, written by a journalist who has been pretty well all over the world. The book is full of interest, both to the naturalist and to the human biologist. What the author says about Lake Baikal will set the zoologist crazy to go there.

CLEARED FOR STRANGE PORTS.

By Mrs. Theodore Roosevelt, Sr., Mrs. Kermit Roosevelt, Richard Derby and Kermit Roosevelt.

Charles Scribner's Sons

$3.00 $5\frac{3}{4} \times 8\frac{1}{2}$; xi + 254 *New York*

As its title would indicate this book written by four members of the Roosevelt family tells of travels and adventures in many lands. There is, in connection with the accounts of hunting trips, a certain amount of information as to habits and behavior of big game, notably elephants and tigers. But somehow these writings lack the touch which our experts in natural history associated with the Roosevelt name. T. R. was a significant, if not a great, naturalist.

MARINE BORERS AND THEIR RELATION TO MARINE CONSTRUCTION ON THE PACIFIC COAST. *Being the Final Report of the San Francisco Bay Marine Piling Committee.*

Edited by C. L. Hill and C. A. Kofoid.

University of California Press

$4.00 net (paper) *Berkeley*

$5.00 net (cloth)

$7\frac{1}{4} \times 10\frac{1}{2}$; ix + 357

The sections of this report are historical (32 pp.), hydrographic (15 pp.), engineering (115 pp.), chemical (25 pp.), and biological (156 pp.). The biological section includes chapters on the classification of the shipworms of the Pacific Coast, morphology of the shipworm, the boring habit, the biology of *Teredo navalis*, the biology of other Pacific shipworms, the occurrence of rock boring mollusks in

concrete, and on *Limnoria* and its allies. There are numerous excellent illustrations.

AN ECOLOGICAL STUDY OF SOUTHERN WISCONSIN FISHES. *The Brook Silversides (Labidesthes sicculus) and the Cisco (Leucichthys artedi) in Their Relations to the Region.*
By Alvin R. Cahn. University of Illinois Press
$1.50 7 x 10½; 151 (paper) *Urbana*

The author has studied in considerable detail the habits of the brook silversides and the cisco. His results, particularly with reference to the daily migrations of the silversides, are interesting and important. He finds that in addition to being positively phototropic, the fish are markedly sensitive to change in pH, and that the daily migration can be accounted for as an attempt to maintain a pH equilibrium of approximately 7.7.

BIRDS OF THE OCEAN. *A Handbook for Voyagers. Containing Descriptions of All the Sea-birds of the World, with Notes on their Habits and Guides to their Identification.*
By W. B. Alexander. G. P. Putnam's Sons
$3.50 3¾ x 6¾; xxiii + 428 *New York*

A well illustrated handbook for the identification of all the seabirds of the world. There are also chapters dealing with the different oceans and the breeding areas of the seabirds found in them. Any voyager or resident at the seaside would find this book useful.

UNSERE KÄFER.
By Max Wolff. Ullstein
0.85 marks 4¼ x 7; 137 (paper) *Berlin*

A popular treatise on beetles from a rather high-toned nature study point of view. Outline figures of common species are given as an aid to identification. The ecologist will find this a handy little book to have about, though it is intended for the amateur.

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung XI.*
Edited by G. Grimpe and E. Wagler.
Akademische Verlagsgesellschaft
11.20 marks *Leipzig*
6 x 8½; 124 (paper)

Previous parts of this valuable work have been noticed from time to time in these pages. The present section covers the following groups: *Pterobranchia*, by C. J. van der Horst; *Chaetognatha*, by W. Kuhl; *Kinorhyncha*, by A. Remane; *Pantopoda* (supplemental article), by J. Meisenheimer; *Tardigrada*, by O. Rahm; *Anoplura Pinnipediorum*, by L. Freund.

BIOLOGICAL SURVEY OF THE UPPER MISSISSIPPI RIVER WITH SPECIAL REFERENCE TO POLLUTION. *From Bulletin of the Bureau of Fisheries, Vol. XLIII, 1927, Part II. Document No. 1028.*
By A. H. Wiebe.
U. S. Government Printing Office
10 cents *Washington*
7⅞ x 11; 33 (paper)

PRODUCTION AND DISTRIBUTION OF COD EGGS IN MASSACHUSETTS BAY IN 1924 AND 1925. *From Bulletin of the Bureau of Fisheries, Vol. XLIII, 1927, Part II. Document No. 1032.*
By Charles J. Fish.
U. S. Government Printing Office
15 cents *Washington*
7⅞ x 11; 46 (paper)

These two papers will be of particular interest to the ecologist. The teacher of

evolution can get from these papers, particularly the second, some first-hand data to put before his classes as to what the "struggle for existence" really means.

ANNOTATED LIST OF FISHES COLLECTED IN THE VICINITY OF GREENWOOD, MISS., WITH DESCRIPTIONS OF THREE NEW SPECIES. *From Bulletin of the Bureau of Fisheries, Vol. XLIII, 1927, Part II. Document No. 1027.*
By Samuel F. Hildebrand and Irving L. Towers. U. S. Government Printing Office
15 cents *Washington*
$7\frac{1}{2}$ x $10\frac{7}{8}$; 32 (paper)

Chiefly of taxonomic and ecological interest.

BEAVER HABITS AND EXPERIMENTS IN BEAVER CULTURE. *U. S. Department of Agriculture Technical Bulletin No. 21.*
By Vernon Bailey.
U. S. Government Printing Office
20 cents *Washington*
$5\frac{7}{8}$ x $9\frac{1}{8}$; 49 (paper)

A brief account of the habits of the beaver with some interesting information as to raising them in captivity.

PROGRESS IN BIOLOGICAL INQUIRIES 1926. *Including Proceedings of the Divisional Conference January 4 to 7, 1927. Bureau of Fisheries Document No. 1029.*
By Elmer Higgins.
U. S. Government Printing Office
25 cents *Washington*
$5\frac{7}{8}$ x $9\frac{1}{8}$; 166 (paper)

This report of the scientific work of what used to be called the U. S. Fish Commission contains a good deal of material of interest to the general biologist especially the student of growth problems and of ecology.

LEHRBUCH DER PROTOZOENKUNDE. *Eine Darstellung der Naturgeschichte der Protozoen mit Besonderer Berücksichtigung der Parasitischen und Pathogenen Formen. Fünfte Auflage. I. Teil. Allgemeine Naturgeschichte der Protozoen.*
By Franz Doflein. Rewritten and revised by Eduard Reichenow. Gustav Fischer
21 marks *Jena*
7 x $10\frac{1}{8}$; iv + 436 (paper)

This new edition of the general biological part of Doflein's well known text is a fine piece of work, which should be in every zoological laboratory. It is beautifully printed, both as to text and illustrations.

BOTANY

MYCORRHIZA. *An Account of Non-Pathogenic Infection by Fungi in Vascular Plants and Bryophytes.*
By M. C. Rayner. Wheldon and Wesley, Ltd.
\$2.25 $6\frac{1}{8}$ x $9\frac{3}{4}$; x + 246 *London*

The author discusses the various lines of research which have been carried on in this interesting field. In the opinion of the writer "there can be no doubt that recent investigations by means of pure cultures have tended to support the view that the possession of mycorrhiza is frequently of benefit to the vascular hosts, the nature and extent of such benefit depending upon the physical conditions of the environment and the physiology of the association in individual cases." The book is well illustrated and has an extensive bibliography. It is essentially

a reprint of a series of articles recently appearing in the *New Phytologist*.

MUSHROOMS AND TOADSTOOLS. *An Account of the More Common Edible and Poisonous Fungi of Canada.*
By H. T. Güssow and W. S. Odell.
Division of Botany, Dominion Experimental Farms
$1.00 8¼ x 10; 274 *Ottawa*

This account of the higher fungi by the Dominion Botanist of Canada "is not intended as a 'learned treatise,' but is meant to appeal to students as well as nature lovers, who wish to know the many odd or beautiful forms of fungous growth they may happen upon in their country rambles." Most of the species described —nearly two hundred in number—also occur in the United States. The book is illustrated with two color plates and 126 plates of excellent photographs, and includes recipes for cooking mushrooms, directions for mushroom culture, a section on poisoning by fungi, bibliography, glossary, and indices.

CLIMATIC CYCLES AND TREE-GROWTH. *A Study of the Annual Rings of Trees in Relation to Climate and Solar Activity. Carnegie Institution of Washington Publication No. 289. Vol. II.*
By A. E. Douglass.
Carnegie Institution of Washington
$2.75 (paper) *Washington*
$3.75 (cloth)
6¾ x 10; vii + 166

The annual rings of trees seem obviously designed to furnish a record of climatic history, as soon as we have learned to interpret them. The present volume gives an excellent account of the technique of obtaining the record, and of its interpretation as at present developed. It must be admitted that much work has still to be done before the interpretation of the record can be regarded as reliable; but the results already obtained are full of promise.

DONNÉES RÉCENTES SUR LES MICROBES ANAÉROBIES ET LEUR RÔLE EN PATHOLOGIE.
By M. Weinberg and B. Ginsbourg.
Masson et Cie
35 francs 6¾ x 10; 291 (paper) *Paris*

A comprehensive review of the work done on pathogenic anaerobes during and since the World War. The volume is issued as a monograph of the Pasteur Institute. The bibliography, which is classified under broad subject headings, covers 47 pages of fine print. The book will be a valuable addition to every bacteriological library.

THE USEFUL PLANTS OF THE WORLD.
By Willard N. Clute.
Willard N. Clute and Co.
$1.50 5¾ x 8½; v + 86 *Joliet, Ill.*

This is a practical kind of book discussing the various plants used for foods, condiments, beverages, drugs, dyes, gums, soaps, textiles, wood products and even those used for decorative purposes. At the back of the book there is a list of economic species, but there is no index.

BEAUTIFUL FLOWERS OF KASHMIR.
By Ethelbert Blatter.
John Bale, Sons and Danielsson, Ltd.
21 shillings *London*
5⅝ x 8⅝; xv + 198

This book contains the description of a

selection of the more common and more beautiful flowers found in Kashmir. There are many colored illustrations, every genus being represented by at least one species. The paintings give evidence of real talent in faithfully rendering posture, form and color of the plants.

A TEXTBOOK OF SYSTEMATIC BOTANY.
By Deane B. Swingle.
McGraw-Hill Book Co., Inc.
$2.00 $5\frac{3}{4}$ x 9; xiii + 254 *New York*

This text is to be used in the study of taxonomy. It is divided into two main parts. The first deals with the principles and rules upon which systematic botany is based and the second describes some sixty families of spermatophytes.

FORESTRY IN SWEDEN. *Trade Promotion Series No. 56.*
By Emil Kekich.
U. S. Government Printing Office
10 cents *Washington*
$5\frac{3}{4}$ x $9\frac{1}{8}$; iv + 27 (paper)

A brief description of forest management in Sweden.

LANDWIRTSCHAFTLICHE SAMENKUNDE. *Ein Schlüssel zum Bestimmen der kleinkörnigen Kultursamen sowie der wichtigsten Unkrautsamen.*
By W. Brouwer. *J. Neumann-Neudamm*
10 marks $6\frac{7}{8}$ x $9\frac{3}{4}$; 130 *Berlin*

Keys, supplemented by photographic illustrations not so well reproduced as they should have been, for the identification of the seeds of agricultural plants and weeds. A useful reference work for the general botanist as well as for the seed analyst, for whom it is particularly intended.

ATLAS DER SAMENKUNDE. 23 *Tafeln mit 625 Abbildungen der Samen der wichtigsten Klee-und der verbreitetsten Unkräuter. Verzeichnis der im Atlas für Samenkunde wiedergegebenen Samenarten mit kurzer Angabe ihres Vorkommens.*
By Prof. Freckmann and Dr. Brouwer.
J. Neumann-Neudamm
24 marks *Berlin*
23 plates; catalogue 16 pp.

Superb heliotype reproductions of greatly enlarged photographs of the common grass and weed seeds. This atlas will be invaluable in any botanical laboratory or agricultural experiment station.

MORPHOLOGY

STRUCTURE DES MUSCLES STRIÉS. *Étude Microcinématographique des Contractions Normales et Atypiques des Muscles et du Myocarde.*
By R. Lutembacher. *Masson et Cie*
45 francs $6\frac{1}{4}$ x $9\frac{1}{8}$; 154 (paper) *Paris*

Unquestionably the potentialities of the moving picture camera as an aid to biological research are at this present moment only dimly envisaged. But anyone who has seen Dr. Carrel's remarkable pictures of his tissue cultures cannot but be impressed with the possibilities which lie in this technique. The present volume deals with a study of the structure, development, and functional activity of striated muscle, by the cinematographic method. A number of interesting new observations are recorded, though no final general conclusions of a novel character are established.

PHYSIOLOGY

ALUMINUM COMPOUNDS IN FOOD. *Including a Digest of the Report of the Referee Board of Scientific Experts on the Influence of Aluminum Compounds on the Nutrition and Health of Man.*
By Ernest E. Smith. *Paul B. Hoeber, Inc.*
\$7.00 6 x 9; xii + 378 *New York*

For anyone interested in the composition and value of food stuffs this book should prove interesting. The author discusses the occurrence of aluminum in the various food stuffs and the effects of their use. Many of his own researches are given as well as the data and conclusions of others. At the end of a chapter of discussion of the material the opinion is expressed that alum baking powders are no less wholesome than any other variety. The terrific battle now waging between the Baking Powder Boys has at least the value to the world in general that it has led to compilations of the pertinent physiological and biochemical literature regarding the effects upon living things of aluminum compounds and tartaric acid and its derivatives, likely to be of considerable use to biologists in general.

LE MÉCANISME DU CŒUR ET SES ANOMALIES. *Études Anatomiques et Électrocardiographiques.*
By Émile Géraudel. *Masson et Cie*
55 francs *Paris*
$6\frac{5}{8}$ x $10\frac{1}{4}$; vii + 285 (paper)

The purpose of this book is to develop a new theory of the causes of the heart beat. The author holds that structurally the bundle of His and the sino-auricular node are identical; and that accordingly their functions should be the same. He considers them both as motor centers, the one for the ventricle, the other for the auricle. Fundamentally they are independent, but are coordinated by the internal circulation of the heart. He draws extensively in support of his claims on evidence from pathological conditions, as revealed by the electrocardiogram and as shown by postmortem examination. Whether his theory is sound is a question for specialists to decide.

THE BASIS OF SENSATION. *The Action of the Sense Organs.*
By A. D. Adrian.
W. W. Norton and Co., Inc.
\$2.50 $5\frac{1}{2}$ x $8\frac{3}{8}$; 122 *New York*

With the development of the vacuum tube amplifier it has become possible to investigate minute changes in electric phenomena with a high degree of accuracy. The present volume gives an account of Dr. Adrian's investigations on the action of the sense organs, as revealed by the electrical changes set up in the nerves. It is an interesting and instructive account of research in a particular field; the author has deliberately confined himself to his own field, and has not attempted any general review or summary of other work on the sense organs.

FOOD AND HEALTH. *An introduction to the Study of Diet.*
By A. Barbara Callow.
Oxford University Press
\$1.00 $4\frac{3}{4}$ x $7\frac{1}{8}$; 96 *New York*

This is a readable little book well designed to give to intelligent laymen some idea of the basic principles in dietetics.

On page 13, we view with alarm the fact that "Cannibalism is certainly more desirable as regards proteins than is a strict diet of vegetarianism. The cannibal

gets all the necessary amino-acids in the exact proportions required, but the vegetarian is in serious danger of missing some essential." As a particularly atrocious example of pernicious British propaganda we recommend this to the perusal of Mayor Thompson.

Physiologists will be interested to learn that in the officer's mess in the army such topics as religion, politics, and women are traditionally tabood; heated argument may arise and digestion may thereby suffer.

PHYSIOLOGY.
By V. H. Mottram.

W. W. Norton and Co., Inc.
$3.00 $5\frac{3}{4} \times 8\frac{3}{8}$; 279 *New York*

This is an outline of physiology written for the general reader interested in the functions of the human body. The author, a distinguished physiologist, writes with literary charm as well as scientific authority. The book is an unusually fine example of the popularization of science at its best.

THE PHYSIQUE OF WOMEN IN INDUSTRY. *A Contribution Towards the Determination of the Optimum Load. Industrial Fatigue Research Board Report No. 44.*
By E. P. Cathcart, E. M. Bedale, C. Blair, K. Macleod and E. Weatherhead. With a special section by Sybil G. Overton.

His Majesty's Stationery Office
5 shillings *London*
$6 \times 9\frac{3}{4}$; vi + 140 (paper)

While intended primarily as an investigation into industrial practice, this report contains a considerable amount of anthropometric material of more general interest. Measurements were made on 4366 women, of height, weight, arm length, distance of finger tips from ground, lumbar pull, hand grip, and arm crush, and the data analyzed statistically. There is also an investigation of the metabolic cost of carriage of loads, with special reference to the manner of carriage. As might be anticipated, it is found that the disposition of the load in large measure determines the physiological cost. We note and like the sort of practicality, shall we say, of certain of the measurements taken.

A COLLEGE TEXTBOOK OF HYGIENE
By Dean F. Smiley and Adrian G. Gould.
The Macmillan Co.
$2.00 $5\frac{1}{4} \times 7\frac{3}{4}$; xiv + 333 *New York*

A textbook of hygiene for college students concerned chiefly with personal hygiene. The book is written for the most part in non-technical language making it especially suited for use in elementary courses. Furthermore the advice about such difficult matters as alcohol and sex is, on the whole, refreshingly sane, probably too much so to please the uplifters. Reading lists follow each chapter and a glossary of technical terms is given at the end of the book.

ACIDOSE ET ALCALOSE. *Physiologie. Pathologie. Thérapeutique.*
By Marcel Labbé and F. Nepveux.
Masson et Cie
30 francs $6\frac{1}{4} \times 9\frac{1}{4}$; 296 (paper) *Paris*

This volume deals with the hydrogen ion equilibrium of the human organism. There are chapters on methods of pH determination; on the physiologic mechanism of acid-base equilibriums; and on the different forms of acidosis and alkalosis and their treatment. There are bibliographies under each head. The book gives a good account of the present state of our knowledge of the subject.

PATHOLOGICAL PHYSIOLOGY OF INTERNAL DISEASES. *Functional Pathology.*

By Albion W. Hewlett. Revised in Memoriam by his Colleagues, Thomas Addis, George DeF. Barnett, Walter W. Boardman, Ernest C. Dickson, Henry G. Mehrtens, Williams Ophuls, Jay M. Read, Howard F. West, Harry A. Wyckoff.

D. Appleton and Co.
$8.50 *New York*
$6\frac{1}{2} \times 9\frac{3}{4}$; xxxiii + 787

A second edition of this admirable text, revised *in memoriam* by the author's colleagues at Stanford University. It reviews the main elements of normal human physiology and considers the mechanism of the more common clinical disorders. The ordinary medical curriculum suffers from the lack of any systematic course in functional pathology and a reading of this book will help remedy the defect.

THE PHYSIOLOGY OF EXERCISE. *A Text-book for Students of Physical Education.*

By James H. McCurdy. *Lea and Febiger*
$3.00 net $5\frac{7}{8} \times 9\frac{1}{4}$; 270 *Philadelphia*

The second edition of this text book for students of physical education has been thoroughly revised and new material has been added, including the results of the original work of Dr. A. V. Hill and others.

BIOCHEMISTRY

KOLLOIDCHEMIE DER STÄRKE.

By M. Samec. *Theodor Steinkopff*
30 marks (paper) *Dresden*
32 marks (bound)
$6\frac{1}{4} \times 9\frac{5}{8}$; xix + 509

This book forms the second volume of what is ultimately to be a great reference *Handbuch der Kolloidwissenschaft in Einzeldarstellungen*, of which the general editor is Prof. Wolfgang Ostwald. It is a thorough and abundantly documented *résumé* of the present state of knowledge of the physics and chemistry of the starches. It will be a valuable reference work in any biological laboratory, as well as to the specialist in the colloid field.

MIKROMETHODIK. *Quantitative Bestimmung der Harn-, Blut-, und Organbestandteile in Kleinen Mengen für klinische und experimentelle Zwecke.*

By Ludwig Pincussen. *Georg Thieme*
6 marks $5\frac{1}{4} \times 7\frac{3}{4}$; 200 (paper) *Leipzig*

The fourth revised and enlarged edition of a standard guide to microchemical technique. A useful book.

STOFFWECHSEL UND ENERGIEWECHSEL.

By H. W. Knipping and Peter Rona.

Julius Springer
15 marks *Berlin*
$5\frac{1}{2} \times 8\frac{5}{8}$; vi + 268 (paper)

The third part, dealing comprehensively with the general subject of metabolism, of Rona's excellent textbook of laboratory practise in physiological chemistry. A useful, well illustrated book.

HISTOCHEMIE DER HAUT.

By P. G. Unna. *Franz Deuticke*
20 marks *Leipzig*
$6\frac{1}{2} \times 9\frac{3}{4}$; vi + 163 (paper)

A detailed discussion of staining methods for the chemical differentiation and determination of the different histological elements of the skin. It is a

valuable contribution to the general subject of cell chemistry, apart from its special interest to dermatologists. It is abundantly and extremely well illustrated with colored figures printed in the text.

HISTOLOGIE UND CHEMIE *der Lipoide der weissen Blutzellen und ihre Beziehung zur Oxydasereaktion, sowie über den Stand der modernen Histologie der Zelllipoide.*

By Ernst Sehrt. *Georg Thieme*
6 marks *Leipzig*
$5\frac{1}{4} \times 8\frac{1}{8}$; 53 + 6 plates (paper)

A morphological and biochemical study of the lipoid granules in leucocytes. The author concludes that white blood corpuscles (neutrophile and eosinophile leucocytes, Mast cells, mononuclears and transition cells) contain lipoid granules as normal constituents of their cytoplasm. There are six colored plates.

RECENT ADVANCES IN BIOCHEMISTRY. *Second Edition.*

By John Pryde. *P. Blakiston's Son and Co.*
$3.50 *Philadelphia*
$5\frac{1}{4} \times 8$; ix + 379

The first edition of this book was noticed here in September, 1927. In the present edition a new chapter has been added on the rôle of tyrosine; and numerous other minor additions have been made in other places.

SEX

THE TRUTH ABOUT BIRTH CONTROL BY FAMOUS AUTHORITIES.

By Bernard Bernard.
Health and Life Publications
$1.75 $5 \times 7\frac{1}{2}$; 166 *Chicago*

This book has been put together by Bernard Bernard, D. Sc. (Phys.), M.S.P., M.P.C. We can see no scientific or other merit in it except as a source book for an investigator of the uplift. For example:

> In human beings, life is only capable of being fully expressed where the act may voluntarily be for the creation of immortality, and otherwise for the inspiration and uplift that it gives. (p. 110).

And from a chapter by Clara Glover, L.L.A. (Hons.), A.C.P. (Hons.):

> The most unfortunate thing in this world is that the average human being obtains his information as to the most vital facts of life from scraps of conversation of the ignorant, or else from the filthy humor of perverts. (p. 115). . . . . Children have very delicate minds, and any vulgarization of the subject may influence the child throughout the whole lifetime. (p. 116). . . . . In years to come it is going to be recognized that qualifications for parenthood are not merely adulthood, but that in order to raise a child properly, it is necessary to have a complete understanding of psychology, biology, physiology, economics and sociology. (p. 117).

SEX PROBLEM IN INDIA. *Being a Plea for a Eugenic Movement in India and a Study of all Theoretical and Practical Questions Pertaining to Eugenics. With a foreword by Margaret Sanger.*

By N. S. Phadke.
D. B. Taraporevala Sons and Co.
6 Rs. $4\frac{3}{4} \times 7\frac{1}{4}$; xii + 348 *Bombay*

A broad and objective title for what is in fact a little book, limited in scope and propagandist in nature. The author, who is professor of mental and moral philosophy in Rajaram College, Kolhapur, disarms criticism by acknowledging that he cannot claim thoroughness of treatment; he wishes only to furnish the reader some material to think about. The thoughts do not promise to be genial, being about the dismal state of affairs in India as regards births, deaths, and marriages. Birth and death rates are

inordinately high; marriages of the female take place at pitifully young ages. The results are deplorable and to be remedied by (1) the abolition of child marriage, (2) the teaching and practice of birth control, (3) the discouragement of dysgenic marriages, and (4) the advocacy of eugenics. The author finds approval for his recommendations in modern social philosophy as well as ancient Indian writings. As a scientific document, the book is, of course, not important.

PSYCHOLOGY AND BEHAVIOR

BRAIN AND MIND *or The Nervous System of Man*.

By R. J. A. Berry. *The Macmillan Co.*
$8.00 6 x $9\frac{1}{4}$; xii + 608 *New York*

A noted neuropathologist called to testify at the trial of an alleged murderer was given the brain of the deceased. "Doctor," said the attorney, "what was the victim thinking of when he died?" As regards the psychologic interpretation of neurologic structure, the lawyer was only somewhat more sanguine than the author of this book. Throughout are expressed such sentiments as the following:

> From the neuronic standpoint all human individuals may be divided into three great groups. The *cerebral aments* who swell the ranks of our prisons, gaols, reformatories, and asylums, though it must not be supposed that all such inmates are aments. *Normal neuronic* individuals who constitute the vast majority, and the *multi-neuronic geniuses* with more than their fair share of neurons.
>
> There can be no question that when the importance of referring all nervous and clinical phenomena to the neuronic arc is more generally recognized, there will be a corresponding improvement in therapy.

In spite of reiterated denials of the writer, it seems generally understood and accepted by medical men that behavior has a necessary basis in nervous structure. This would appear to be ample justification for advancing the study of neuroanatomy, without calling in heroic and quite unfounded claims for it as a solvent of psychological problems. The shoe is really on the other foot; most medical men fail to deal adequately with behavior problems, because of their attempt to understand them completely in terms of neurology. There is need in the medical curriculum for the study of behavior *qua* behavior.

Depleted of the interspersed propaganda, the book is a fair neuroanatomical text, conventional in the main as regards individual topics, but somewhat novel in matters of arrangement, and containing a short, inadequate section on the nervous system in health and disease.

THE MATRIX OF THE MIND.

By Frederic Wood Jones and Stanley D. Porteus. *University of Hawaii*
$4.00 6 x 9; viii + 457 *Honolulu*

The authors hold that the mind really has a brain, and the brain a mind, and propose to make a study which will blend both. The reunion is effected by the pronouncement that there is an external nervous system consisting of sensory skin and sense organs, and an internal nervous system consisting of brain and spinal cord. The latter are simply cells of the skin of the back, which, residing in a quiet region during embryological development, and not otherwise occupied, were tucked into the depths of our body. It is quite evident therefore that our central nervous system is made up of buried skin and our skin of unburied nervous system. And what follows more logically than that there is an adjustment between external behavior and nervous structure? The

bird that has a gay exterior has an internal system likewise gay, and he parades and makes a show and indulges in actions and habits in accord with his bright color. "Did we ever see a sparrow which perked and minced and flirted as a robin is wont to do? I doubt it; and if we did, the whole thing would appear ridiculous on the part of the sparrow. The sparrow has no equivalent to a scarlet patch in his central nervous system and to behave as though he had would be incongruous and absurd."

Reginald, the Office Boy, says that: "In that regard the bird would appear to resemble the scientists who propound such a theory." But we do not agree. Whatever Prof. Wood Jones writes is sure to be original and stimulating, and we are all for him on that account. Time will tell whether his theories are right or not, and in the meantime we render thanks that there are still a few scientific men able and willing to say something original.

SELECTED PAPERS OF KARL ABRAHAM, M.D.

Translated by Douglas Bryan and Alix Strachey. *The Hogarth Press*

30 shillings $5\frac{3}{4} \times 9$; 527 *London*

Karl Abraham was the first true psychoanalyst in Germany. He propounded its doctrines with great pertinacity against vigorous opposition as early as 1907, and sponsored the Psychoanalytic Association in Berlin. He was among the most active members of the International Association, and after 1913 led the opposition against Jung. When the latter resigned, he was appointed provisional president, and in 1924 was elected to the regular presidency, to which he was reelected in 1925. In his death, the same year, at the age of forty-eight, psychoanalysis suffered the most severe personal loss of its history.

This volume contains all of his important work, not previously published in English, except his study on Amenhotep. There is the usual abundance of reference to such subjects as anal character, oral eroticism, coprophilia, mother's bowel, etc., etc., etc., which for the innocent reviewer, not yet attuned to the beauties of the psychoanalytic mythology, makes depressing reading.

A bibliography and index are included.

THE MENTAL LIFE. *A Survey of Modern Experimental Psychology.*

By Christian A. Ruckmick.

Longmans, Green and Co.

\$2.00 $5\frac{1}{2} \times 7\frac{3}{4}$; x + 253 *New York*

This introductory text to psychology is written for the general reader as well as for use in elementary courses. There are review questions and selected bibliographies at the end of each chapter. There is also a group of classified references at the close of the book. We recommend our readers to take a look at the frontispiece, which is alleged to be a picture of "the boundary between the mental and the physical worlds." Once more we are inhibited from making appropriate comments because THE QUARTERLY REVIEW OF BIOLOGY is a family magazine.

PSYCHOLOGICAL CARE OF INFANT AND CHILD.

By John B. Watson, with the assistance of Rosalie R. Watson.

W. W. Norton and Co., Inc.

\$2.00 $5\frac{1}{8} \times 7\frac{1}{2}$; 195 *New York*

Everybody has always known that

John Watson is a courageous man. He has proved it again, by taking his behaviorism out of the safe cabinet of philosophic abstraction and using it as the basis of telling the world the technique for the bringing up of a happy child. The authors believe, probably rightly, that the psychological care of the infant is in some ways more important than the physiological care, in that once a child's character has been spoiled no one can say that the damage can ever be repaired.

THE MINDS OF ANIMALS. *An Introduction to the Study of Animal Behavior.*
By J. Arthur Thomson. George Newnes, Ltd.
2 shillings net *London*
$5 \times 6\frac{1}{4}$; 206

An introductory book for the use of those interested in animal behavior. Examples are given of what might be considered "mind" throughout the animal kingdom beginning with the amoeba. Such entertaining subjects as; "Can animals tell the time?" and "Do animals ever laugh?" are discussed. The author holds that the mental aspect of animal life is not restricted to control of activities and the like but may "manifest itself in feelings, in concrete purposes, in music and artistry."

AN EXPERIMENTAL STUDY OF THE OLFACTORY SENSITIVITY OF THE WHITE RAT. *Genetic Psychology Monographs, Vol. III, No. 1.*
By John R. Liggett. Clark University
$2.00 *Worcester, Mass.*
$5\frac{5}{8} \times 9\frac{1}{4}$; 64 (paper)

The experiments recorded here are interpreted by the author as indicating that "olfaction apparently does not have a very important rôle in the daily life of the rat." Whether this conclusion follows from the data seems to us questionable. He found that in learning mazes and in the discrimination box the rats were apparently not aided by odors; but that they were able to locate food buried under sawdust with considerable success. Which of these forms of activity is more important in daily life seems to us to depend on whether one is a psychologist or a white rat.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE CIPHER OF ROGER BACON.
By William R. Newbold. Edited with foreword and notes by Roland G. Kent.
University of Pennsylvania Press
$4.00 *Philadelphia*
$6\frac{1}{8} \times 9\frac{1}{4}$; xxxii + 224

Shooting fleas with an elephant gun is difficult. The late Professor Newbold devoted an enormous amount of ingenuity and labor to deciphering what he thought were Roger Bacon's ciphers. The cipher, as he developed it, is enormously complex, extremely difficult to unravel, and, if we are not greatly in error, entirely impossible to use. In fact, we are ready to place a small wager that the cipher has its origin in the mind of Professor Newbold and not in that of Roger Bacon. Our reasons for this opinion are partly technical; that is, the system of cryptography here expounded seems to us entirely fantastic, and one which no one would use in practice. A further reason for scepticism is to be found in the known history of cryptography. Until considerably later than Bacon's time, the systems used were of the simplest.

But what seems the most persuasive evidence against Professor Newbold, and

what prompted the possibly rude remark about fleas, is that he has overlooked two perfectly good and genuine ciphers in the material he offers. These are to be found in the *Tractatus Trium Verborum*, reproduced in his Plate IX, and in the Vatican manuscript, Lat. 3102, reproduced in his Plates XXVII and XXVIII. The first of these consists of three passages, concluding each of the three chapters, and described by Newbold as "series of meaningless letters." Actually they are in a very simple substitution cipher, using the following alphabet:

Plain Text	A	B	C	D	E	F	G	H	I	L	M	N	O	P	Q	R	S	T	U	V
Cipher	Z	A	D	E	C		I		H		M	N	L	O		R	T	V	S	

The first passage runs:

Explicit	MZINSM et	ORHMSM	MCNEZDHSM	RLIERH	AZDSN
	magum	primum	mendacium	Rogeri	Bacun
	ZE HLGZNNC OZRHD				
	ad Iohanne (m) Paric				

(The final D in cipher is clearly a scribe's error for T, reading Paris.)

The Vatican manuscript is even more entertaining, and more damaging to Professor Newbold's sense of proportion. This is apparently an alchemical document, which he labors over greatly, and eventually converts into a theological treatise. The original text contains obvious cipher passages, together with symbols which we take to be alchemical signs. These latter are outside our field of knowledge; but it has proved entertaining and easy to translate the cipher portions. The alphabet used is the following:

	A	B	C	D	E	F	G	H	I	L	M	N	O	P	Q	R	S	T	U
Cipher	C	B	[12]	[8]	D	F	G		L	Z	M	N	R	P	Q	[6]	Y	T	S.
			[10]													[7]			
			[11]													[9]			

The numbers refer to some of the arbitrary symbols (called by Newbold Tironian signs); the numbering is Newbold's, but it would appear that he had found more different signs than were actually used. Also we find that his reading of some letters differs from that obviously necessary to make sense.

Not being an authority on alchemy, we do not feel competent to expound the deciphered text; but with the alphabet just given, anyone who cares to may amuse himself with it.

THE OPUS MAJUS OF ROGER BACON.
A translation by Robert B. Burke.
University of Pennsylvania Press
2 volumes, $10 *Philadelphia*
$6 \times 9\frac{1}{4}$; xiii + 840

We have all heard of Bacon as the forerunner of modern experimental science, but most of us have had to take our opinions secondhand. The present translation affords an opportunity for direct acquaintance, and should interest everyone who is curious about the history of science. We fear, however, that Bacon's reputation will suffer; as long as he remained a man of mystery, he could be regarded as a superhuman genius, to whom details like the invention of the telescope and microscope were matters of routine. A reading of the Opus Majus will destroy many such pleasant illusions, and provide the basis for a sounder estimate of Bacon's importance.

It is unfortunate that the present volume lacks annotations. It is extremely difficult for the reader with no special knowledge of the period to gather how much of the Opus Majus is original with Bacon and how much he has obtained from Avicenna, Alhagen, Aristotle, and others. It is to be hoped that Professor Burke will give us a supplementary volume of notes.

QUANTA OF EVOLUTION.
By Henri Hinoko. *Henri Hinoko*
50 cents *61 Battery St., Seattle*
$5\frac{3}{4} \times 9$; 26

Opus 3 in a series by Henri Hinoko (*né* Henry Allen, Seattle, Washington), of which No. 2 was noticed previously in these columns. The foreword reports progress. Whereas the first work, on gravitational theory, had a perfect no-sale record, of the second, on racial old age, the author gave away 495 copies and sold one. We despair of doing the present book justice in the short space available; every page, nay every paragraph, contains a novel idea of revolutionary import. A small random sample yields:

> Now we are ready for the hook-up of ice-ages with our assumed explanation of gravitation. As the Solar System revolves thru its particular orbit in the Local Star System it suddenly enters into a high pressure zone. I say "suddenly" advisedly because the Quantum Theory is assumed to apply to celestial spaces as well as elsewhere and the sudden flashing forth of nova or "new stars" is sufficient evidence at least of its possibility. This high pressure zone causes a certain amount of compression within the Solar System, resulting in an increase of internal heat within its constituent parts. This increased heat, in the case of the Sun, causes a shift in the solar spectrum from the infra-red end to the ultra-violet end of the spectrum. This is in harmony with the unanimous conclusions of the astrophysicists that the bluish suns are the hottest and the reddish suns the coolest. This condition leads to the anomalous result that the hottest suns, giving off the shortest wave lengths, produce at a distance less heat due to the relative less amount of the longer wave lengths.
>
> It is doubtful whether the very light blondes ever produce first-rate men.
>
> A new explanation of our beards, and hair on our heads, namely that it affords ingress for atmospheric electricity to the motor centers of the body.

Alas the book concludes: "I do not take my views of Racial Old Age and of Quanta of Evolution too seriously. What's the use? If I am right then nearly everybody else in America must be wrong. And, if by chance there should be a general acceptance in America of most of my views, that would prove I must be mostly wrong."

Before such invulnerable logic we acquiesce; Henri's noble efforts seem doomed to frustration.

PRINCIPLES IN BIO-PHYSICS. *The Underlying Processes Controlling Life Phenomena and Inner Evolution.*
By Conrad Richter. *Good Books Corporation*
\$1.00 *Harrisburg, Pa.*
$5 \times 7\frac{1}{4}$; 86 (paper)

Like many paradoxers Mr. Richter loves quasi-mathematical symbolism. Thus

Cn + #1, CA/B, R or RE, KCn + #2,

as a section heading leaves the reader the least bit in doubt as to the underlying thought, especially when the context shows that KCn is not a misprint for potassium cyanide. But it really is quite simple. What this odd symbolism tells us is this:

> A boy has been angered by a whipping and threat from his Father, (Cn + #1). To satisfy his desire for relief, he packs a few clothes in a small bag and begs a ride from a motorist going West, from which he derives some satisfaction and thrill, (R and RE). After an hour of the ride, however, his anger appears to be less keen than it had been, (Inharmony of Cn + #1 has been lowered by CA/B from R and RE). He begins to think how far he is from home and how much his mother may worry, (KCn + #2 touched off by both OC and CC). After a time he finds he is tired, that his wanderlust has disappeared and that he is now concerned over getting back home, (KCn + #2 has yielded enough energy to relax Cn + #1).

The book expounds a theory which is developed about energy in relation to life, mind, and behavior. We greatly fear that, unfortunately, all the other biologists in the world are out of step with Mr. Richter.

GALLIO *or The Tyranny of Science.*
By J. W. N. Sullivan. *E. P. Dutton and Co.*
$1.00 $4\frac{1}{4} \times 5\frac{7}{8}$; 57 *New York*

Another addition to the now numerous members of the To-day and Tomorrow Series, initiated by J. B. S. Haldane's *Daedalus*. The first volume was a delightful excursion of the imagination into the realms of the seemingly possible. The later ones are more concerned with the present, and particularly the evils thereof. This one is an earnest protest against that "materialistic" science born in the Victorian age which imposed a picture of purposelessness, governed by hard immutable law, as a complete description of the universe. It was an unwarranted presumption, because really science deals with abstractions that have to do only with a limited part of the universe, and fails to reach such truth as is gleaned by poets, mystics and musicians. The fact is coming out now in the newer developments of science and scientific philosophy. Scientists in high standing are admitting the inadequacy of materialistic concepts.

This thesis, as presented, is not convincing, but much that is said *en passant* about the limitations of the scientist as a person will be recognized as justified by those who know him in the flesh.

THE EVIL RELIGION DOES.
By Morrison I. Swift. *The Liberty Press*
$2.00 $5\frac{1}{2} \times 7\frac{3}{4}$; 111 *Boston*

Morrison I. Swift dislikes Sabbatarianism (p. 5), pacifism (p. 17), militarism (p. 17), Christianity (*passim*), Chinese immigration (p. 19 et seq.), trusting in God (p. 26), Jews (*passim*), monopolists (p. 38), Zionists (p. 43), rabbis (p. 54), Jesus (p. 57), God (p. 58), priests (p. 60), Fundamentalists (p. 52), Modernists (p. 62), Catholics (p. 65), parochial schools (p. 80), Protestantism (p. 89), Roger Babson, (p. 93), social inequality (p. 95), conscientious objectors (p. 101), Christian Science (p. 104), and lawyers (p. 105). We have possibly missed one or two. The book is a savage attack on all these, but primarily on religion. We doubt, however, that it will cause many church-memberships to lapse.

THE RISE OF MODERN PHYSICS. *A Popular Sketch.*
By Henry Crew.
The Williams & Wilkins Co.
$5.00 $5 \times 7\frac{1}{4}$; xv + 356 *Baltimore*

A short history of physics, written for the laity. Some of the more recent developments are omitted—relativity, for example—but most of the important parts of the subject are brought reasonably up to date. The mathematics of the subject is reduced to such a point that one wonders why the few differential equations which appear—without any apparent reason—were not omitted altogether.

There is a three page bibliography, and references in the text to primary or secondary sources for the various subjects treated. Altogether a useful book for its intended purpose.

THE TURNING POINT.
By Richard J. Flanagan.
Perry and Elliott Co.
$5 \times 7\frac{5}{8}$; 54 (paper) *Boston*

The author's final conclusions are:

> Disease is an external evidence of internal uncleanliness.
>
> Internal uncleanliness and disease are the same.

The name "Disease" should be abandoned and "Internal uncleanliness" substituted.

There is but ONE cause of disease—indiscriminate water drinking.

There is but ONE cure—cut it out.

Anti-saloon League please copy.

NOTRE MISÈRE SCIENTIFIQUE. *Ses Causes. Ses Remèdes. L'Appel du Roi.*

By Q. M. Quaeris and collaborators. *Fr. Saey*
10 francs *Bruxelles*
$6\frac{1}{2} \times 10\frac{1}{4}$; 57 (paper)

A polemical document said to be about the sad conditions in the Belgian universities in general, relative to scientific research, but really devoted to the obviously sadder case of one Professor Lecat, a mathematician. Those who like university politics will find it interesting.

THE POCKET GUIDE TO SCIENCE. *A Book of Questions and Answers on the Facts of Modern Science.*

By E. E. Free. *Popular Science Monthly*
75 cents $3\frac{1}{4} \times 5$; 284 *New York*

A small book written for the public at large containing common questions on all kinds of scientific matters and answers to these questions.

THE COST OF BIOLOGICAL BOOKS IN 1928

By RAYMOND PEARL

Institute for Biological Research, Johns Hopkins University

AT THE end of the first volume of The Quarterly Review of Biology (Vol. I, pp. 605–608 1926) was inaugurated the plan of reporting annually on the cost of the books which had been received during the year. The present paper continues this plan with the report of book costs for the year 1928.

For the purpose of price comparison the books are classified by origin as follows:

I. *The United States.* Here are put all books published by strictly, or primarily, American publishers. Naturally the majority of books reviewed during the year have had this origin just as in earlier years.

II. *Germany.* In the number of books sent in by publishers for review, Germany stands next to this country.

III. *English-American.* In this group are placed the books which are manufactured and published in the first instance in England by publishing houses which have *branches* under their own name (not merely agents) in this country. The American branch imports the books into this country and distributes them here, priced in dollars rather than shillings.

IV. *England.* In this class are placed books published in England, priced in shillings, and available in this country only by direct importation, by the individual or through an agent.

V. *France.* This group includes all books published in France and her colonies.

VI. *Other Countries.* Here are placed all books published in any other country than those specified above.

VII. *United States Government.*

VIII. *British Government.*

Table 1 gives, for each of these eight rubrics, (*a*) the total number of pages in the books received for review; (*b*) the total cost of these books in dollars, foreign prices being converted to dollars on the basis of the exchange prevailing when the books were received; (*c*) the average price per page *in cents*.

In order to facilitate comparison in respect of book prices, Table 2 has been prepared. In this table the following items are included: (*a*) the average price per page, in cents, for the years 1926–1928; (*b*) the absolute changes in average price per page, in cents, between 1926 and 1928, and between 1927 and 1928, a + sign denoting an *increase* in 1928 as compared with the earlier years, and a − sign denoting a *decrease;* (*c*) the percentage differences of the 1928 average price per page from those of 1926 and 1927, the + sign again indicating that the books were on the average higher in price in 1928 than they were in the earlier years, and the − sign that they were lower.

The first point to be noted from Table 1 is the continued increase in the total amount of book material noticed in The Quarterly Review of Biology. The total number of pages reviewed in 1928 is 122,154, an increase of 19.6 per cent over 1927, and of 47.9 per cent over 1926. Plainly available space will put a limit to

this increase. In fact it seems likely that it will not be desirable to increase significantly the amount of space given to book reviews in future volumes over that allotted in Volume III, though if our readers have ideas on this subject we shall be glad to hear them.

Coming to the prices given in Table 1, the first thing which strikes the eye is that the "Other countries" group stands at the top, with an average price per page far out of line with the rest of the table. This average is, however, not a fair representation of the actual facts. Its high value of 2.16 cents per page is to an undue extent determined by two expensive books, one costing $26.70, the other $35.00. Each contains many plates. Leaving these two books out of the reckoning, as may fairly be done on the ground that they are special treatises not belonging in the average run of biological books, the average price per page of the "Other countries" books becomes 1.13 cents as shown in Table 2. With this change Germany heads the list, its average topping slightly that for the English-American books, which in the two previous years have been the most expensive.

The sample of British Government publications reviewed this year was small and the books were higher priced per page, on the average, than either American or English commercially published books. But the emphasis here should be on the smallness of the sample, which undoubtedly does not give an entirely fair representation of the case. It must however be said that in 1927 the British Government publications which we received were relatively high in price, four times as high, in point of fact, as United States Government publications. As usual the biological books published by the United States Government stand at the bottom of the list, and next to them the French books. French scientific books are still marvelously cheap, as compared with the commercially published books of the rest of the world.

Turning now to a consideration of the trends in prices shown in Table 2 it should be first noted that two groups show a consistent and, to the consumer, pleasing record. These are England and the United States Government. In both cases the average price per page each year is lower than it was the year before. In 1928 the English commercially published books cost 4.4 per cent less per page than they did in 1927, and 14.8 per cent less than they did in 1926. The corresponding percentage decreases in prices for United States Government books were 12.5 and 32.3 per cent.

TABLE 1

Prices of biological books, 1928

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
Other countries.	5,177	$111.93	2.16
Germany	20,964	310.78	1.48
English-American	2,766	40.25	1.46
British Government	517	6.50	1.26
United States	64,810	741.88	1.14
England	10,602	115.36	1.09
France	11,750	52.70	0.45
U. S. Government	5,568	11.65	0.21

On the other hand there has been, during these three years, an equally consistent and steady increase in the average price per page of commercially published German and French biological books. German biological books, judged by our samples, were 23.3 per cent higher in 1928 than in 1927, and 35.8 per cent higher in 1928 than in 1926. The corresponding percentage increases in the price of French biological books were 25.0 and 28.6 per cent. In the case of the French books the absolute

price is so low that the percentage increase does not matter practically. The German case is not so good, however. Their biological books were absolutely the highest priced in 1928, and also are increasing in price at the most rapid rate, so far as may be judged from our sample during the years 1926 to 1928 inclusive. While it is easy to understand and appreciate the economic considerations which lead to increasing costs of commercially published books in France and Germany, it is a question whether in the latter country the publishers are not dangerously close to the point in their pricing of scientific books where they will bring into operation that other sad economic law of which the effect is that absolute returns diminish. There can be no great profit in publishing books at such high prices that nobody buys them. Biological books commercially published in the United States were higher in 1928 than in either 1926 or 1927, but by small amounts.

If all the books noticed in THE QUARTERLY REVIEW OF BIOLOGY in 1928, regardless of origin, are lumped together and compared with all the books noticed in earlier years it works out that the average price per page in 1926 was 1.097 cents, 1.030 cents in 1927, and 1.095 cents in 1928, omitting the two very expensive books noted above. This indicates an *increase* in average price of 6.3 per cent in 1928 as compared with 1927, but a *decrease* of 0.2 per cent as compared with 1926. On the whole it is obvious that, in the period reviewed, no violent price changes have occurred in either direction, if one envisages a generally balanced library of current biological books.

In each of these reports on the cost of books attention has been called to the high price of books in our English-American group, and it has been pointed out that, so far as concerns such books, our benevolent government, in its wisdom, puts a heavy tax upon American scholarship. Regarding this subject Mr. George P. Brett, of the Macmillan Company in New York, has published recently an important pamphlet. In this pamphlet Mr. Brett says:

> In the year 1913 a new Tariff Bill was enacted in which Congress, evidently with the laudable intention in mind of reducing the cost of such books to students and others, lowered the duty on them from

TABLE 2

Comparison of the prices of biological books in 1926, 1927, and 1928

ORIGIN	AVERAGE PRICE PER PAGE 1926	AVERAGE PRICE PER PAGE 1927	AVERAGE PRICE PER PAGE 1928	CHANGE + OR − FROM 1926 TO 1928		CHANGE + OR − FROM 1927 TO 1928	
				Absolute	Relative	Absolute	Relative
	cents	*cents*	*cents*	*cents*	*per cent*	*cents*	*per cent*
English-American	1.55	1.39	1.46	−0.09	−5.8	+0.07	+5.0
Other countries	1.51	0.78	1.13*	−0.38	−25.2	+0.35	+44.9
England	1.28	1.14	1.09	−0.19	−14.8	−0.05	−4.4
United States	1.12	1.09	1.14	+0.02	+1.8	+0.05	+4.5
Germany	1.09	1.20	1.48	+0.39	+35.8	+0.28	+23.3
British Government	—	0.96	1.26	—	—	+0.30	+31.3
France	0.35	0.36	0.45	+0.10	+28.6	+0.09	+25.0
U. S. Government	0.31	0.24	0.21	−0.10	−32.3	−0.03	−12.5

* With two special treatises omitted as explained in the text.

25 per cent to 15 per cent. That it was the intention of Congress to reduce the duty on these classes of books mostly or solely is evidenced by the fact that in the new bill many other classes of books which are competitive from the American publishers' and printers' point of view were raised from the normal rate in various ways.

Apparently the action of Congress in reducing the duty met with objection on the part of the Treasury, and in 1918–19, through its board of Appraisers and Customs Courts, the question of the value of the imported books on which the new duty of 15 per cent should be assessed was again raised, and, notwithstanding the arguments of the publishers—arguments which convinced the Board of General Appraisers in the years 1902–03—the Customs Court declared that the duty should be assessed not upon the cost of the books but upon a fictitious price, which in many or most cases was double and in some cases more than double the actual cost of the books to the importers, the effect being that the books in question now paid a greater amount of duty under the reduced rate as authorized by Congress than was previously paid on such books at the higher rate of 25 per cent and the price of these books to students and others were of necessity greatly increased.

There seems no reasonable excuse for this successful attempt on the part of the Treasury, through its Customs Court, to nullify the deliberate intentions of Congress, and the students and others who use books to which this new ruling applies apparently rejoiced too soon at the attempt of Congress to reduce their burdens. As has been pointed out above, books imported from abroad now cost these consumers more in relation to their foreign price than was the case before the duty was nominally reduced by Congress from 25 per cent to 15 per cent.

Even although under a strictly narrow legal interpretation of the wording of the Tariff Act, backed by a report from a customs agent which was biased, incomplete, and inaccurate, there is perhaps warrant for the ruling which was put into effect, it seems without doubt that common sense should govern the matter, as was the case in 1903, rather than a merely technical, narrow, legal ruling on the actual words used, the evident intention of Congress having been to reduce the duty, whereas the ruling of the Customs Court above referred to actually increases it, and the benevolent intention of Congress has been frustrated by the bureaucratic methods of the Treasury.

This sad tale, which is of direct and personal interest to every reader of THE QUARTERLY REVIEW OF BIOLOGY, is one more evidence of the nobility, grandeur, and intelligence with which the government of this country operates.

In concluding these notes for the present year I should like again to emphasize that the statistical nature of the basic data is such as not to permit wide generalization. We are dealing here only with very small samples of books in general, and with by no means all of the strictly biological books. Indeed for some of the countries our samples are only small fractions of the biological works there published. So the reader must be cautious in the kind of conclusions he draws from these annual reviews of the experience of THE QUARTERLY REVIEW OF BIOLOGY regarding book prices.

INDEX